Fishery Bulletin

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Seattle, Washington

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Fishery Bulletin

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FIELD CRITERIA FOR SURVIVAL OF ANCHOVY LARVAE: THE RELATION BETWEEN INSHORE CHLOROPHYLL MAXIMUM LAYERS AND SUCCESSFUL FIRST FEEDING[1]

REUBEN LASKER[2]

ABSTRACT

Northern anchovy larvae, *Engraulis mordax*, produced by laboratory-spawned fish, have been used to detect concentrations of larval fish food in situ along the California coast. First-feeding larval anchovies, whose development was controlled by temperature manipulation aboard ship, were placed in samples of Los Angeles Bight water taken from the surface and from chlorophyll maximum layers. Feeding by larvae in water from the surface was minimal in all experiments but extensive feeding occurred in water from the chlorophyll maximum layers when these contained phytoplankters having minimum diameters of approximately 40 μm and which occurred in densities of 20 to 40 particles/ml. In March and April 1974, the chlorophyll maximum layer along the California coast from Malibu to San Onofre (a distance of about 100 km) consisted chiefly of a bloom of the naked dinoflagellate *Gymnodinium splendens*, a food organism known to support growth in anchovy larvae. Copepod nauplii and nonliving particles were never in high enough concentration or of the proper size to be eaten by the larvae. A storm which caused extensive mixing of the top 20 m of water obliterated the chlorophyll maximum layer and effectively destroyed this feeding ground of the larval anchovy.

Probably the major problem confounding fishery scientists interested in rational management of fisheries is an inability to predict recruitment failure (Gulland 1973) despite the vast amount of laboratory and field work on food chain analysis leading to fish production which has occupied many workers in marine studies for the past two decades (Steele 1970). Gulland (1973) asks the most pressing question, "Can a study of stock and recruitment aid management decisions?" and in the same article answers "No." This pessimistic reply is given because, as he says, "there is no method which is likely to be generally successful, [because] the most promising depends on lengthy and costly collection of data, probably extending over a long period." The work reported in this paper suggests an approach which has not been previously used in fishery research as far as I am aware, and which, I believe, makes the answer Gulland has given somewhat less pessimistic than when he made it.

However, it is generally agreed among fishery biologists that large spawning populations of fish do not ensure subsequent large year classes, and conversely, small spawning populations occasionally give rise to exceptionally large classes (Hjort 1926). Hjort (1914) postulated that these variations in year class strength are probably due to differential mortality of the larvae. He believed, for example, that the larvae of the Norwegian herring, *Clupea harengus*, suffered huge mortalities resulting in small year classes when there was a lack of food for the first-feeding larvae. The attractiveness of this hypothesis has generated a number of laboratory studies (see, for example, Lasker et al. 1970) which have shown that the density of larval food must be higher than that usually found at sea in order to obtain even moderate larval growth and survival. For an in-depth discussion of the larval "critical period" as affected by food see May (1974), and for a review of laboratory attempts to rear fish larvae, refer to May (1971). The conclusion that the mean density of larval food organisms in the ocean is generally too low to support reasonable survival of fish larvae through metamorphosis, is also substantiated by data from field surveys (Beers and Stewart 1967, 1969). Thus, despite extensive efforts in quantitative marine food chain analysis, it is yet to be demonstrated whether, where, and to what extent there are rich feeding areas in the sea for larval fishes.

[1]MARMAP (Marine Resources Monitoring, Assessment, and Prediction) Contribution No. 17.

[2]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92037.

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As a new approach to this problem it is the purpose of this study to show how laboratory-spawned fish larvae can be used to detect larval feeding grounds at sea and to point out some of the ways this technique might be used to provide the link between marine food chain research and stock and recruitment predictions in fisheries; the latter by determining what the environmental conditions at sea must be with respect to larval fish food to result in a good or bad survival year for particular species of fish larvae.

Because it is essential to the general methodology of using larval fishes as assay organisms for the fitness of seawater as larval fish feeding grounds, in the following I describe some background information on maturation and spawning of anchovies in the laboratory; the methods used for feeding larval anchovies; and the laboratory-determined criteria for feeding already known for the larva of this species. A description of the field work is then given, concluding with a discussion of the criteria which can be used to judge the fitness of the larval anchovy's environment.

THE NORTHERN ANCHOVY

In the California Current, the major pelagic fish population at present is that of the clupeoid *Engraulis mordax*, the northern anchovy. This species is found from British Columbia, Canada to Cape San Lucas, Baja California and extending west about 600 km. Although the anchovy has a protracted spawning season from December to August, about three-quarters of its spawning occurs in the winter and spring months of January, February, March, and April. The factors affecting larval mortality of clupeoids have been investigated in a number of laboratories throughout the world (Holliday and Blaxter 1963) including my own. Recently, it has been possible to intensify laboratory research at the Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service because of the continuous availability of anchovy larvae. This has been made possible by inducing sexual maturation of adults in the laboratory resulting in daily spawning and fertilization of anchovy eggs throughout the year. Details of this maturation and spawning technique are given by Leong (1971) and Lasker (in press). The availability of first-feeding larvae hatched from laboratory-spawned eggs has made possible the development of a technique whereby specific areas of the ocean could be examined for their potential as larval feeding grounds, and criteria established to characterize parts of the ocean as good or bad areas for larval survival.

LABORATORY-DETERMINED CRITERIA FOR SUCCESSFUL LARVAL ANCHOVY FEEDING

A background of information on larval anchovy feeding is available from a number of studies and was used to guide this investigation.

1. *Particle size at first feeding appears to be critical.* First-feeding anchovy larvae (standard length 3.5 mm) have small mouths and require a food particle about 50 μm in diameter, although particles larger than 100 μm may be taken (Berner 1959). Smaller particles may not be visible to the larvae. Berner (1959) reported that anchovy larvae smaller than 4 mm long taken in plankton tows had eaten particles ranging in length from 24 to 186 μm. However, over 70% of the food in their intestines was between 60 and 80 μm long.

2. *The number of particles per unit volume in the anchovy larva's environment must be above a minimum concentration.* O'Connell and Raymond (1970), using natural plankton as food, showed that the survival of first-feeding anchovy larvae was dependent, in their experiments, on the number of micronauplii per unit volume available to the larvae. Successful first feeding, as pointed out by Hunter (1972), also depends on a sufficiently high density of food particles to compensate for the low capture efficiency (about 10%) exhibited by anchovy larvae when they begin to feed.

3. *The kind of food organism determines survival and growth.* Lasker et al. (1970) fed a variety of phytoplankters and zooplankters to first-feeding anchovy larvae. Only one phytoplankter of those tested, *Gymnodinium splendens*, supported growth and gave relatively good results in survival experiments when compared with larvae fed natural plankton. The rotifer *Brachionus plicatilis*, although not found in the anchovy's normal habitat, also could be used as a laboratory food for older anchovy larvae and a small proportion of first-feeding larvae (Theilacker and McMaster 1971; Hunter 1972).

4. *The greater the concentration of food particles, the more frequent are the feeding strikes made by anchovy larvae; consequently the greater the success in capturing food.* Although examination of field-caught anchovy larvae reveal very few with

any food in their intestine (Arthur 1956; Berner 1959), this seems to be a result of rough handling due to capture in a plankton net and subsequent preservation with Formalin[3] which causes almost all anchovy larvae to defecate (Kjelson et al. 1975). In the laboratory a high proportion of anchovy larvae which had never seen a food particle will strike at and ingest them provided there is a high enough concentration of the right size food particles. Hunter and Thomas (1974) have shown that the rate of larval anchovy feeding increases with increasing food density.

Despite the success of O'Connell and Raymond (1970) and Kramer and Zweifel (1970) who were able to rear anchovy larvae using micronauplii concentrated in wild plankton samples, the quantities needed by the larvae seemed inordinately higher than the concentration of nauplii reported by Beers and Stewart (1967) for the euphotic zone of the California Current. It was possible, of course, that concentrations of nauplii exist in dense aggregations. Beers and Stewart (1970a) reported that nauplii concentrate in or immediately above chlorophyll maximum layers off the California coast. However, no concentrations have been identified which are high enough to support anchovy larvae (e.g., 1/ml). On the other hand, Lasker et al. (1970) showed that anchovy larvae would feed and grow on a diet of the dinoflagellate *G. splendens*. The fact that blooms of a variety of phytoplankters are known to occur in the California Current, particularly in the spring, suggested that phytoplankton cells were more likely to provide the particle size and cell density essential to survival and growth of first-feeding anchovy larvae. For these reasons, inshore chlorophyll maximum layers were selected as possible fruitful areas to investigate for larval feeding.

METHODS

To determine areas in the sea where high concentrations of living particles might be present, a pump was used to bring water on board from known depths. The hose from the pump was lowered below the surface by means of a metered winch. The water was pumped through a Turner fluorometer in the ship's laboratory to measure chlorophyll *a* and other fluorescing substances. Chlorophyll *a* was extracted from water samples taken at each station from different depths and the fluorescence profile adjusted to reflect only chlorophyll *a* (Kiefer and Lasker 1975).

A school of approximately 700 sexually mature northern anchovies, maintained in the aquarium of the Southwest Fisheries Center, La Jolla Laboratory, produce about 1,000 fertilized eggs per day. The number of eggs can be increased by injections of gonadotrophins to stimulate massive spawning in individual fish (Leong 1971). With temperature control of development (Lasker 1964), larvae in first-feeding condition can be made available whenever desired. Thus, preliminary to a cruise, development of embryos and larvae can be accelerated or retarded by temperature manipulation to ensure that on each day of the cruise there will be at least several hundred larvae ready to feed.

Prior to each of the cruises described here, fertilized eggs at the same stage of development were sorted into liter jars containing seawater previously filtered through a 5-μm pore size Cuno Aquapure filter, and the jars were immersed in water baths at suitable temperatures. For transport to the ship insulated chests were used, and on board a temperature-controlled room was continually adjusted between 13° and 18°C to insure that feeding larvae would be available on specific days. Recent studies have shown that newly feeding larvae have only about 2½ days after the yolk sac is absorbed to get sufficient food or they will die (Lasker et al. 1970).

Experiments to determine if samples of seawater contained suitable food for anchovy larvae were done in cylindrical, 8-liter jars wrapped with dull black cardboard and set on black plastic. Above the jars a bank of four "daylight" fluorescent lights were suspended which illuminated the surface of the jars at approximately 2,152 lux. When a sample of seawater was brought into the ship's laboratory it was permitted to warm slowly to room temperature. Larvae were added to 5 liters of seawater by pouring them from the incubation jars. Dilution of the 5 liters by the larval incubation water was corrected by concentrating the contents of an additional liter of seawater to a few milliliters with fine mesh netting and by adding the concentrate to the whole.

A gentle air stream was directed onto the surface of the water in each experimental vessel to ensure mixing of the water. Control experiments on shipboard with cultured organisms indicated that this had little effect on the larvae.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Two cultured food organisms, *G. splendens* and *B. plicatilis*, were used aboard ship to determine if any particular batch of test larvae was in good condition and would feed. Details on the culture of these organisms are given by Thomas et al. (1973) for *G. splendens*, and Theilacker and McMaster (1971) for *B. plicatilis*. Usually a control 5-liter seawater sample was seeded with one or the other cultured organism and a feeding experiment with larvae run concurrently with samples of natural seawater.

Larvae were permitted to feed for 8 h then siphoned out and sucked down onto a membrane filter (pore size 0.8 μm) using a vacuum pump. This rapid removal of larvae from the experimental containers and their fast immobilization on the filters prevented defecation. After air drying, microscopic examination of the transparent larvae permitted counts to be made of larvae which had been feeding and those which had not. The relative proportion of feeding to nonfeeding larvae was subsequently correlated with sizes of the food particles, chlorophyll content, species composition, and the number of particles available to the larvae.

A 1-liter subsample of each seawater sample was preserved with Formalin (final concentration 5%) (Beers and Stewart 1970b). Later the particles in the preserved seawater were settled out and the species enumerated. The method of Utermöhl (as described by Lund et al. 1958) was used to concentrate organisms from known volumes of preserved seawater, usually 100 ml. At least 100 cells larger than 20 μm in diameter were counted from each settled water sample.

On a cruise of the NOAA RV *David Starr Jordan*, 18-21 March 1974, a 16-channel electronic particle counter with a 280-μm pore, Coulter Counter Model Ta, was used to determine the size distribution and numbers of sized particles in seawater samples used for feeding experiments. Only particles 20 μm and larger were counted. Very good agreement was obtained between the electronic counter particle counts and those obtained with the inverted microscope. A comparison is shown in Figure 1. The speed of counting and sizing particles makes the multichannel particle sizing instrument desirable for rapid field assessment of larval fish food organisms. Because the electronic counter was unavailable for two subsequent cruises. 8-12 and 22-23 April 1974, the results for these are given from microscope counts only.

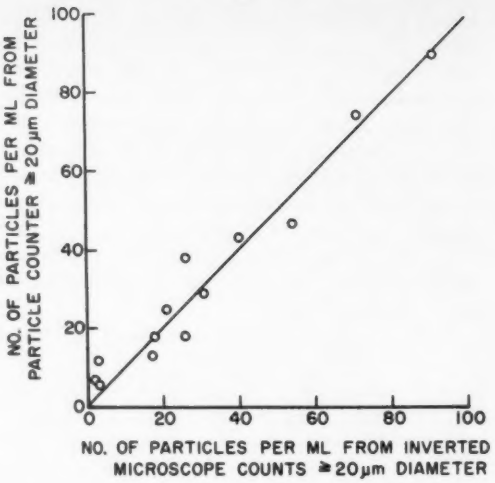

FIGURE 1.—Comparison between instantaneous particle counts per milliliter taken with Model Ta Coulter Counter and mean particle count per milliliter observed through an inverted microscope. A 100-ml sample was concentrated and at least 100 particles of the dominant organism were counted in any visual field. Only particles larger than 20 μm were counted.

To ascertain if anchovy larvae were present at particular depths, plankton tows were taken with a 0.333-mm mesh, 0.5-m mouth diameter net. Because an opening and closing net was unavailable for this work, an open net was dropped rapidly to the desired depth, towed for 10 min at a maintained wire angle of 45°, then pulled up rapidly. The total proportion of time the net spent in water other than in the desired stratum never exceeded 5% of the total towing time. All larvae captured were measured, sorted to species, and counted. Larval counts were corrected to a comparative volume of 1,000 m^3 (Kramer et al. 1972). A flowmeter in the mouth of the net provided a record of the volume of water filtered.

The shipboard experiments were ordinariy done at temperatures of between 15° and 19°C, whereas concentrations of larval fish food organisms and anchovy larvae were occasionally found between 14° and 15°C. It was desirable, therefore, to determine the feeding response of first-feeding anchovy larvae at different environmental temperatures. Experiments to determine this were identical to those done at sea except that the concentration of the cultured organism *G. splendens* was varied from 5 to 200 cells/ml, and the water temperature was controlled within ±0.2°C.

AREA OF STUDY

This investigation was conducted in the Los Angeles Bight along the southern California coastline from Malibu to San Onofre, between 18 and 21 March 1974. All the stations occupied were over the 20-fathom line except for the Laguna Beach station which was over the 270-fathom contour. Table 1 gives the coordinate positions and Figure 2 shows the relative location of the stations. The San Onofre station was reoccupied on 8 April 1974 to determine the persistence of the chlorophyll maximum layer which earlier had contained relatively large numbers of *G. splendens*. The station was occupied again on 10 April, after a violent wind storm and later on 22-23 April after a period of no storms.

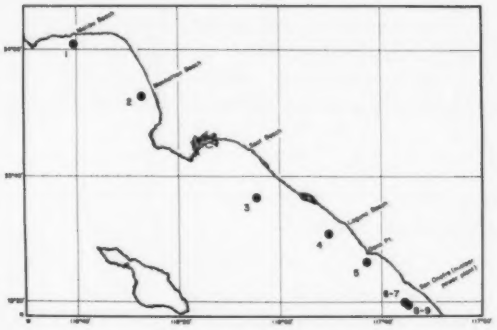

FIGURE 2.–Stations in the Los Angeles Bight.

RESULTS AND DISCUSSION

Shipboard Experiments with First-Feeding Anchovy Larvae

Table 1 provides a summary of the results of feeding experiments with first-feeding anchovy larvae in water from the surface and from the chlorophyll maximum layer or from a depth of about 15 m if no clear chlorophyll maximum was observed. The dominant phytoplankter in the chlorophyll maximum layers was *G. splendens*. For details about *G. splendens* blooms from Baja California, Mexico, and the Los Angeles Bight see Kiefer and Lasker (1975); as reported earlier, Lasker et al. (1970) had demonstrated that anchovy larvae will grow when fed on *G. splendens*.

Also given in Table 1 are the results of a feeding experiment at the San Onofre station on 8 April 1974, 18 days after a chlorophyll maximum layer containing *G. splendens* as the dominant phytoplankter was found. The chlorophyll maximum layer was still present and heavily populated with *G. splendens*. A violent wind storm on 9 April obliterated the chlorophyll maximum layer and no *G. splendens* were seen at this station when it was reoccupied on 10 and 11 April. A comparison of chlorophyll *a* profiles taken before and after the 9 April storm is shown in Figure 3. The results of control feeding experiments are given in Table 2.

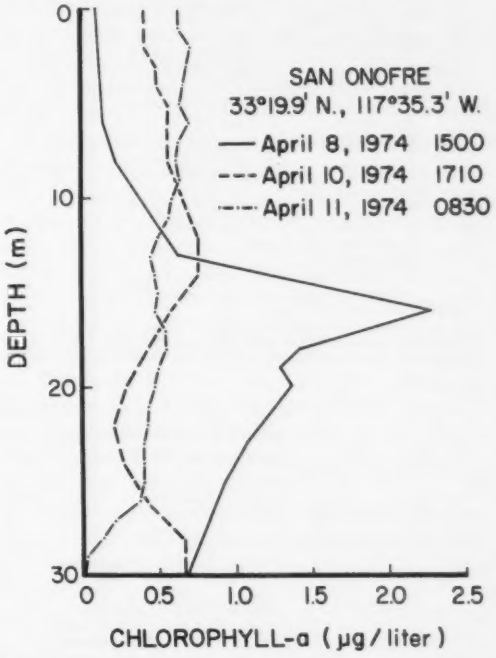

FIGURE 3.–Chlorophyll maximum layers before (8 April 1974) and after (10 and 11 April 1974) a violent wind storm near San Onofre, Calif.

Some anchovy larvae capture a few particles in any concentration of 20- to 100-μm particles over an 8-h period, but experience in the laboratory has shown that feeding on less than 1 particle/h will not sustain a first-feeding larva which becomes weak and dies. Thus, in Tables 1 and 2, two feeding categories are indicated: larvae observed with food organisms packed into the intestine, and

TABLE 1.–Summary of results of 8-h on-board feeding experiments with first-feeding anchovy larvae. *Gymnodinium splendens* appeared in the chlorophyll maximum layers (chl. max.) from Malibu to San Onofre, a distance of approximately 130 km. The subsurface bloom of *G. splendens* at San Onofre persisted until 8 April 1974 (see no. 7 below). A storm on 9 April obliterated the maximum and evidently dispersed the *G. splendens* by wind mixing (see Figure 3).

No.	Date and time A. Surf. temp. B. Chl. max., temp. and depth	Position (lat. N-long. W)	Total number particles/ml 23-37 μm diameter	 >37-299 μm diameter	μg Chl. *a* per liter	Feeding by anchovy larvae Percent of larvae with: ¼ to full gut	 1-8 particles in gut	Number of larvae per experiment
1	20 March 1974, 1250							
	A. 15°C	34°00.8′-118°40.6′	14.2	[1]4.1 (< 1)	[2]1.0	2	15	69
	B. 14.2°C, 12 m	(Malibu)	37.3	38.0 (12)	1.8	23	46	93
2	20 March 1974, 1745							
	A. 15.2°C	33°52.5′-118°27.0′	23.1	6.1 (6)	0.4	0	11	94
	B. 14.5°C, 13.5 m	(Manhattan Beach)	29.8	19.7 (12)	1.3	0	18	49
3	21 March 1974, 0900							
	A. 15.8°C	33°36.5′-118°04.3′	217.9	33.2 (< 1)	0.3	0	12	42
	B. 14.2°C, 16.5 m	(Seal Beach)	53.8	352.0 (380)	42.0	22	24	104
4	21 March 1974, 1340							
	A. -	33°30.8′-117°50.3′	34.0	9.0 (0)	0.6	0	10	20
	B. -, 15 m (no chl. max.)	(Laguna Beach)	29.0	5.7 (0)	0.7	0	11	46
5	21 March 1974, 1715							
	A. 15.5°C	33°26.3′-117°42.8′	18.7	5.9 (< 1)	0.5	[3]5	16	19
	B. -, 15 m	(Dana Point)	55.2	23.2 (5)	1.3	0	69	26
6	21 March 1974, 1900							
	A. 15.2°C	33°19.9′-117°35.3′	9.3	4.0 (< 1)	0.2	0	8	49
	B. -, 19.5 m	(San Onofre)	42.4	47.7 (34)	2.3	9	25	32
7	8 April 1974, 1500							
	A. 17.1°C	33°19.9′-117°35.3′	5.7	9.1 (< 1)	0.2	0	13	23
	B. 14.8°C, 16 m	(San Onofre)	14.0	81.3 (64)	2.3	9	40	58
8	10 April 1974, 1710							
	A. 14°C	33°19.4′-117°34.6′	8.4	14.1 (0)	–	0	12	33
	B. 13.5°C, 14 m (no chl. max.)	(San Onofre)	10.5	23.2 (0)	0.8	0	15	20
9	11 April 1974, 0915							
	A. 13.0°C, 5 m (no chl. max.)	33°19.5′-117°34.6′ (San Onofre)	6.4	10.5 (0)	0.6	0	4	50

[1]( ) = number of *G. splendens* per milliliter.
[2]Particles smaller than 20 μm may have contributed to the elevated chlorophyll *a* at this station.
[3]This 5% figure represents only one larva which filled its intestine ¼ full.

TABLE 2.–Controls for the experiments reported in Table 1. Surface water was seeded with *Gymnodinium splendens* or *Brachionus plicatilis*. In each instance the results showed that the larvae on shipboard were competent to feed. Feeding time was 8 h.

Date	Species seeded	Number particles/ml	Feeding by anchovy larvae Percent of larvae with: ¼ to full gut	 1-8 particles in gut	Number of larvae per experiment
20 March 1974	*B. plicatilis*	40	29	45	72
8 April 1974	*G. splendens*	100	27	13	30
10 April 1974	*G. splendens*	100	32	22	46

those with eight or fewer particles in the intestine after an 8-h feeding period. The largest proportion of larvae did not feed at all, a result common to laboratory experiments as well. The feeding intensity at Malibu, Seal Beach, and San Onofre is typical of first-feeding anchovy larvae in laboratory experiments seeded with a like number of suitable size particles, e.g., *G. splendens*.

The data presented in Table 1 show that the criteria for larval anchovy feeding determined by laboratory experiments are the same when freshly obtained seawater is tested as a source of larval anchovy food. Large numbers of particles smaller than 37 μm in diameter did not stimulate feeding in anchovy larvae. This was particularly apparent at Seal Beach on 21 March; surface water having 218 particles/ml smaller than 37 μm in diameter but with low chlorophyll *a* did not stimulate anchovy larvae to feed. Conversely, the bloom of *G. splendens* in the chlorophyll maximum layer produced heavy feeding larvae tested in shipboard experiments. Furthermore, even with particles

having the right diameter for feeding, a minimum concentration of perhaps between 25 and 50 cells/ml was needed.

The Effect of Temperature on Feeding

The chlorophyll maximum layers along the coast were characterized by temperatures between 14° and 15°C, which is lower than the optimum temperature for feeding and growth in anchovy larvae (16°C). Because shipboard experiments were done at temperatures higher than those found in the chlorophyll maximum layers it was desirable to determine if the minimum particle count at which first-feeding larvae were stimulated to feed was in any way reduced by lower temperatures. Figure 4 illustrates the results of experiments which show that at 14°C, the food particle count must be higher than 20 cells/ml before significant feeding can occur over an 8-h period. At the higher temperature tested, 18°-19°C, food particle counts of between 5 and 20 particles/ml may stimulate feeding. However,

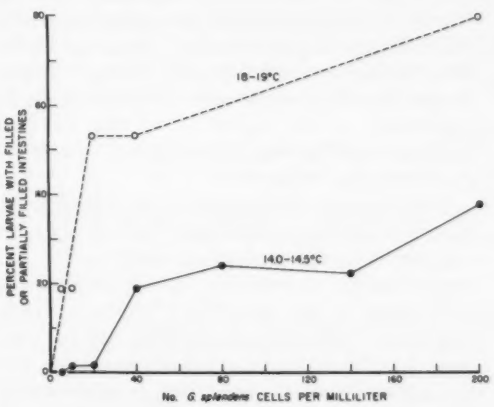

FIGURE 4.—The effect on larval anchovy feeding of different concentrations of food at two temperatures. Each experiment began with 100 larval anchovies which were in first-feeding condition and was terminated after 8 h. See text for details.

during the shipboard experiments, particle counts of 5-20 cells/ml did not stimulate larval feeding even at the higher temperatures (15°-19°C) of the ship's laboratory (Table 1). This discrepancy may be due to the different kinds of food particles available to the larvae, as well as to other factors related to a larva's inability to capture certain particles as opposed to others. For example, when *Chaetoceros* sp. was present in any of the samples, anchovy larvae did not feed on this phytoplankter, owing probably to the spiny nature of this chain-forming diatom, despite the considerable lengths (longer than 37 μm) of the chains. In the Seal Beach surface sample taken on 21 March 1974, *Chaetoceros* sp. and other chain-forming diatoms made up over 30% of the longer than 37-μm category. This result was confirmed at a station off Imperial Beach, Calif. (lat. 32°34.0′ N; long. 117°10.5′ W) on 11 April where a dense bloom dominated by *Thalassiosira* sp. (37 chains/ml) was found. Chlorophyll *a* at the surface was 4.8 μg/liter and slightly higher, 5.1 μg/liter, at a depth of 7 m. Feeding by anchovy larvae on this organism was virtually nil. Thus, the composition of the stock of phytoplankton appears to be an important factor in the initial feeding of anchovy larvae.

The observations described above indicate that chlorophyll measurements alone, and the indication of a strong chlorophyll maximum layer are not by themselves sufficient criteria for establishing the existence of good conditions for the feeding of anchovy larvae. A cruise of the RV *David Starr Jordan* was made back to the San Onofre station on 22 and 23 April 1974. A sharp chlorophyll maximum layer was discovered there once again and was found to extend seaward for at least 14 km (Figure 5), yet shipboard larval anchovy feeding was negative. Subsequent microscopic examination of the water from these layers indicated that cryptomonads of about 10 μm in diameter dominated the samples in concentrations of 3,400-7,200 cells/ml, a size too small to be fed upon by anchovy larvae.

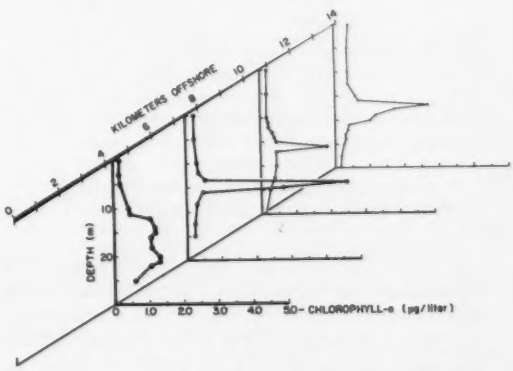

FIGURE 5.—Chlorophyll maximum layers off San Onofre, Calif., 22-23 April 1974.

Vertical Distribution of Anchovy Larvae

At San Onofre on 8 April the chlorophyll maximum layer was due, in part, to a high density of *G. splendens*. Larvae on board ship fed freely in the water from this layer. Judging from the larval feeding and the size and density of the food particles, this chlorophyll maximum layer should have been an ideal place for first-feeding larvae to be found. To test this, plankton tows were made at three depths: within the chlorophyll maximum layer at 16 m, just above the layer at 10 m, and at the surface (see Figure 3). The standard length of anchovy larvae from these tows was measured, and the degree of eye pigmentation noted (full pigmentation indicating a visually competent larva). The results, given in Table 3, show that there was a distinct difference in vertical distribution between the number of first-feeding larvae that could see as opposed to yolk-sac larvae which lack eye pigmentation and could not see.

The surface water contained 2,100 anchovy larve/1,000 m³. Larvae without eye pigmentation outnumbered sighted larvae two to one. At the 10-m stratum above the chlorophyll maximum layer there were 40,000 anchovy larvae/1,000 m³ with larvae capable of seeing outnumbered by eight to one. In the chlorophyll maximum layer 4,900 anchovy larvae/1,000 m³ were present but larvae that could see were about as numerous as those which could not. Although it may be coincidental, the possibility that larvae were actively seeking out areas with food cannot be dismissed.

TABLE 3.–Distribution of anchovy eggs and larvae at three depths off San Onofre, Calif., 8 April 1974.

Stratum	Number of eggs or larvae per 1,000 m³		
	Larvae with pigmented eyes	Larvae with unpigmented eyes	Eggs
Surface	756	1,344	67,200
10 m	4,610	35,804	151,965
16 m	2,004	2,941	60,034

Criteria for Successful First-Feeding by Anchovy Larvae

It is evident from the data presented in this report that the following environmental criteria must be met before first-feeding anchovy larvae can feed successfully in the ocean. Phytoplankton aggregations with over 20 cells/ml must be available at the same time or within 2½ days after the larvae are ready to feed. Individual phytoplankton cells must be about 40 μm in diameter. Successful feeding is dependent on food density so that the higher the concentration of cells, the better the feeding. Monotypic algal blooms are responsible for some chlorophyll maximum layers off the California coast and first-feeding anchovy larvae were found to be living within them. Only some phytoplankters stimulate feeding and support growth of anchovy larvae; for example *G. splendens* is known to support growth while anchovy larvae would not feed on *Chaetoceros* sp. or *Thalassiosira* sp., spiny and/or chain-forming diatoms. Finally, it could not be demonstrated that micronauplii or other microzooplankton contribute significantly to larval anchovy survival during the first week of larval life. Beers and Stewart (1967) reported that in December 1965, the inshore station off San Diego (their station I) contained a maximum of only 30 organisms/liter in the 35 to 103-μm size class. Of these organisms, copepod nauplii and post-nauplii together numbered 7-9/liter, two orders of magnitude lower than that required by anchovy larvae to survive, i.e., 1,000/liter (O'Connell and Raymond 1970). However, it is reasonable to assume that under special circumstances suitable concentrations of micronauplii might serve as a food source for first-feeding anchovy larvae. Nonliving particles larger than 37 μm were not seen and may be insignificant in the nutrition of first-feeding anchovy larvae because of their low concentration in anchovy spawning areas.

It is important to emphasize the transient nature of good feeding conditions. There was a large number of larvae present at depth at the San Onofre station on 8 April 1974, capable of taking advantage of the subsurface bloom of *Gymnodinium*. Furthermore, spawning had been extensive in the entire water column as indicated by the large number of anchovy eggs caught during the same tows (Table 3). Earlier I indicated that a wind storm obliterated the chlorophyll maximum layer at San Onofre on 9 April 1974, and that 8-h shipboard experiments showed the larvae were unable to capture enough food on 10 and 11 April to fill or partially fill their intestines. If my contention is correct, then a large proportion of the larvae which were present as eggs or yolk-sac larvae on 8 April were doomed to die from lack of food after the storm on 9 April because of the dilution and dispersion of suitable larval food organisms.

Although this investigation was confined to first-feeding anchovy larvae, the technique

described here, using laboratory-reared larvae for field tests of possible larval feeding areas, probably can be extended to older larvae and other species as well. An on-board electronic counter can give a rapid first evaluation of particle size and cell numbers. Microscopic examination of subsamples can be used to verify the shipboard counts and give additional information on species composition of phytoplankters. Chlorophyll profiles can be analyzed routinely on most oceanographic vessels. With information on the biology of the larvae being investigated, it may be possible to determine routinely the quality and extent of larval feeding grounds and with comprehensive temporal information on the food of the larvae, the degree of larval mortality due to inadequate food may be predictable.

ACKNOWLEDGMENTS

Thanks go to Eileen Setzler, Anne N. Dodson, Dale Kiefer, and the able crew of the NOAA RV *David Starr Jordan* for their invaluable assistance during this study, and to Richard Eppley for stimulating discussions which led to the examination of chlorophyll maximum layers as possible feeding grounds for larval fish. Roderick K. Leong provided the fish larvae on demand; without his help this study would not have been possible.

LITERATURE CITED

ARTHUR, D. K.
1956. The particulate food and the food resources of the larvae of three pelagic fishes, especially the Pacific sardine, *Sardinops caerulea* (Girard). Ph.D. Thesis, Univ. California, Scripps Inst. Oceanogr., La Jolla, 231 p.

BEERS, J. R., AND G. L. STEWART.
1967. Micro-zooplankton in the euphotic zone at five locations across the California Current. J. Fish. Res. Board Can. 24:2053-2068.
1969. Micro-zooplankton and its abundance relative to the larger zooplankton and other seston components. Mar. Biol. (Berl.) 4:182-189.
1970a. Numerical abundance and estimated biomass of microzooplankton. *In* J. D. H. Strickland (editor), The ecology of the plankton off La Jolla, California, in the period April through September, 1967, p. 67-87. Bull. Scripps Inst. Oceanogr. 17.
1970b. The preservation of acantharians in fixed plankton samples. Limnol. Oceanogr. 15:825-827.

BERNER, L., JR.
1959. The food of the larvae of the northern anchovy *Engraulis mordax*. Bull. Inter-Am. Trop. Tuna Comm. 4:1-22.

BLAXTER, J. H. S., AND F. G. T. HOLLIDAY.
1963. The behaviour and physiology of herring and other clupeids. Adv. Mar. Biol. 1:261-393.

GULLAND, J. A.
1973. Can a study of stock and recruitment aid management decisions? Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 164:368-372.

HJORT, J.
1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 20:1-228.
1926. Fluctuations in the year classes of important food fishes. J. Cons. 1:5-38.

HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. Fish. Bull., U.S. 70:821-838.

HUNTER, J. R., AND G. L. THOMAS.
1974. Effect of prey distribution and density on the searching and feeding behaviour of larval anchovy *Engraulis mordax*. *In* J. H. S. Blaxter (editor), the early life history of fish, p. 559-574. Springer-Verlag, Berl.

KIEFER, D. A., AND R. LASKER.
1975. Two blooms of *Gymnodinium splendens*, an unarmored dinoflagellate. Fish. Bull., U.S. 73:675-678.

KJELSON, M. A., D. S. PETERS, G. W. THAYER, AND G. N. JOHNSON.
1975. The general feeding ecology of postlarval fishes in the Newport River estuary. Fish. Bull., U.S. 73:137-144.

KRAMER, D., AND J. R. ZWEIFEL.
1970. Growth of anchovy larvae (*Engraulis mordax* Girard) in the laboratory as influenced by temperature. Calif. Coop. Oceanic Fish. Invest. Rep. 14:84-87.

KRAMER, D., M. J. KALIN, E. G. STEVENS, J. R. THRAILKILL, AND J. R. ZWEIFEL.
1972. Collecting and processing data on fish eggs and larvae in the California Current region. U.S. Dep. Commer., NOAA Tech. Rep. NMFS CIRC-370, 38 p.

LASKER, R.
1964. An experimental study of the effect of temperature on the incubation time, development and growth of Pacific sardine embryos and larvae. Copeia 1964:399-405.
In press. Induced maturation and spawning of marine fish at the Southwest Fisheries Center, La Jolla, California. Proc. 5th Annu. Workshop, World Mariculture Soc.

LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.
1970. Feeding, growth and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5:345-353.

LEONG, R.
1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69:357-360.

LUND, J. W. G., C. KIPLING, AND E. D. LECREN.
1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia 11:143-170.

MAY, R. C.
1971. An annotated bibliography of attempts to rear the larvae of marine fishes in the laboratory. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-632, 24 p.
1974. Larval mortality in marine fishes and the critical period concept. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 3-19. Springer-Verlag, Berl.

O'CONNELL, C. P., AND L. P. RAYMOND.
1970. The effect of food density on survival and growth of early post yolk-sac larvae of the northern anchovy (*Engraulis mordax* Girard) in the laboratory. J. Exp. Mar. Biol. Ecol. 5:187-197.

STEELE, J. H. (editor).
1970. Marine food chains. Univ. Calif. Press, Berkeley, 552 p.

THEILACKER, G. H., AND M. F. MCMASTER.
1971. Mass culture of the rotifer *Brachionus plicatilis* and its evaluation as a food for larval anchovies. Mar. Biol. (Berl.) 10:183-188.

THOMAS, W. H., A. N. DODSON, AND C. A. LINDEN.
1973. Optimum light and temperature requirements for *Gymnodinium splendens*, a larval fish food organism. Fish. Bull., U.S. 71:599-601.

SPERMATOPHORES AND THELYCA OF THE AMERICAN WHITE SHRIMPS, GENUS *PENAEUS*, SUBGENUS *LITOPENAEUS*

ISABEL PÉREZ FARFANTE[1]

ABSTRACT

The spermatophores of the five species of the American subgenus *Litopenaeus* of the genus *Penaeus*, three in the Pacific–*P.* (*L.*) *occidentalis*, *P.* (*L.*) *stylirostris*, and *P.* (*L.*) *vannamei*–and two in the Atlantic–*P.* (*L.*) *schmitti* and *P.* (*L.*) *setiferus*–are described in detail and illustrated. The spermatophore of *P. vannamei* uniquely lacks a wing and a lateral blade. That of *P. stylirostris* possesses a sac with overlapping walls, the free lateral margin not being attached to the underlying wall throughout most of its length; this spermatophore also exhibits the broadest wing, consisting of a rigid anterior region and a posterior membranous one. The spermatophore of *P. occidentalis* is the only one armed with an anterior lobe, a transverse anterior lamina, and a sclerotized flap. The spermatophores of the Atlantic species are very similar, both possessing moderately broad wings, large caudolateral flanges, and a lateral blade; however, in *P. schmitti* the blade is broad anteriorly, whereas in *P. setiferus* it is very narrow. During copulation, as the males deposit paired spermatophores on the females, the sperm masses are released through anterodorsal ruptures of the sperm sacs and become lodged on the thelycum, protected ventrally by the anterior part of the sacs. The open-type thelycum (sperm receptacle lacking), characteristic of the members of *Litopenaeus*, is unique within the genus *Penaeus*. The thelyca are described in order to facilitate understanding how the compound spermatophores are held in place. The thelycum of each species exhibits at least one obvious typical feature by which it may be easily recognized: that of *P. vannamei* is provided with an inverted troughlike median protuberance on sternite XIII; in *P. occidentalis* it possesses densely set setae over most of sternite XIV; in *P. stylirostris* it is armed with a strong, subpyramidal median protuberance on sternite XIV; in *P. schmitti*, on the other hand, it exhibits paired subparallel anterolateral ridges; and in *P. setiferus* paired crescentic anterolateral ridges are present which, although convergent, do not meet on the midline. In all but one species, thelycal concavities of sternite XIII serve to lodge the sperm masses which protrude from attached spermatophores; however, in *P. occidentalis* spoonlike coxal plates of the third pereopods receive the sperm masses.

The five species of *Penaeus*, subgenus *Litopenaeus*, commonly known as white shrimps, support some of the most intensive and valuable fisheries in American waters. Three species are limited to the eastern Pacific, *Penaeus occidentalis*, *P. stylirostris*, and *P. vannamei*, and two occur in the western Atlantic, *P. schmitti* and *P. setiferus*. Mass rearing experiments to discover methods for artificial cultivation on a commercial scale are being conducted on all five species, and spermatophore-bearing or "impregnated" females are needed for this undertaking. Despite these efforts, and the considerable interest of biologists in the reproduction of these species (including mating, spawning, and fertilization), descriptions of the spermatophores of only two of them and brief notes on a third are available. General features of the spermatophore of *P. setiferus* were presented by both Burkenroad (1934) and King (1948), and an account of that of *P. stylirostris* was given by Cárdenas Figueroa (1952). Subsequently, Ewald (1965) and Pérez Farfante (1969) recorded a few observations on the spermatophore of *P. schmitti*. The spermatophores of the remaining two species, *P. occidentalis* and *P. vannamei*, have not been mentioned previously.

Lack of information on spermatophores of the subgenus *Litopenaeus* is due, at least in part, to the fact that impregnated females are not readily found (Weymouth et al. 1933; Burkenroad 1939; Heegaard 1953). In this exclusively American group, the females possess an open-type thelycum (Burkenroad 1934; Pérez Farfante 1969), lacking a seminal receptacle and consisting, instead, of protuberances, ridges, concavities, or grooves and, occasionally, lamellae on sternites XII to XIV to which the spermatophore is attached. The latter is thus exposed to the surrounding water and might be dislodged during capture, as suggested by Burkenroad (1939), or retained for only a short period after copulation. In the females of all other

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subgenera of *Penaeus*, the thelycum exhibits a seminal receptacle where the spermatophores, deposited by the male, remain well protected until the time of spawning or until the succeeding molt.

Among the extensive collections of the subgenus *Litopenaeus* that I have examined, no females of either *P. occidentalis* of *P. vannamei* carrying spermatophores were found. Four impregnated females of *P. stylirostris* and two of *P. schmitti* in the National Museum of Natural History, Smithsonian Institution, constituted the only material at my disposal when this study was initiated. After several unfruitful attempts to collect spermatophore-bearing females in various localities throughout the range of the Pacific species, I obtained such specimens of the three in the Gulf of Panama in March 1973. I caught an additional one of *P. occidentalis* in the same month off Buenaventura, Colombia. In the fall of 1974, Billy R. Drummond sent me three impregnated females of *P. stylirostris* which had been collected off Costa Rica, and recently Harold H. Webber brought me eight spermatophore-bearing females of *P. stylirostris* and five of *P. vannamei* from the same area. The study of the spermatophore of the Atlantic *P. setiferus* was based largely on one female carrying a complete spermatophore and three additional ones in which paired masses of sperm embraced by winglike processes were present on sternite XIII; these specimens had been caught in the waters of North Carolina, and were made available to me by Austin B. Williams. Recently, further observations were made on four impregnated females, two from Apalachicola Bay, Fla., and two from off Texas, given to me by William H. Clark, Jr. and Kenneth N. Baxter.

The spermatophores of the various species are similar (herein described as when in position on the female), each consisting basically of a roughly semicylindrical hardened sperm sac enclosing a columnar sperm mass (spermatozoa within a viscous fluid) surrounded by a thick "sheath" (King 1948) of gelatinous substance (Figure 1A, B). The sac usually bears an anterolateral aliform process, the wing, and is produced caudally or caudolaterally, in a flange. A lateral flap, variable in width and consistency, extends both along the sac and the flange, or only along the latter, usually attached to a firm, elongate blade, and a hardened but plastic dorsal plate is present on the posterodorsal surface of the spermatophore. Finally, a glutinous material always lies against the flange, adhering to the mesial side of the flap. These various accessories associated with the sperm sac presumably help to anchor the spermatophores to the female.

The wall of the sperm sac consists of three somewhat distinct longitudinal regions: a thick, opaque ventral wall, a mostly thin and translucent lateral wall, and an entirely translucent dorsomesial wall. The heavy ventral wall is produced in a longitudinal mesial lapel, clearly delimited by a line along which the ventral and dorsomesial walls meet. The above terminology is consistently employed in the descriptions that follow.

During copulation, two closely attached spermatophores, which are here referred as the compound spermatophore, are transferred to the female (Figure 1C). Immediately after expulsion from the paired terminal ampullae of the male, each spermatophore joins its mate firmly along the dorsomesial walls of the sacs, thus forcing the mesial lapels to project ventrally from the contiguous ventral walls (Figure 1D). These walls, becoming strongly convex when the compound spermatophore is anchored to the thelycum, are responsible for the podlike appearance of the conjoined paired sacs, which constitute a median double structure referred to below as the geminate body.

If the posterior part of the thorax of live mature males is compressed, the spermatophores are readily expelled through the gonopores situated mesially on the coxae of the fifth pereopods. It then may be observed that the spermatophores leave the ampullae with the anterior end foremost, the surface facing the sternum of the male being the same as that which, through a rotation, comes to lie against the thelycum. Consequently, as Kishinouye (1900) first indicated, the right and left spermatophores on the female originate in the corresponding right and left terminal ampullae of the male. Observations by Hudinaga (1942) on *Penaeus* (*Marsupenaeus*) *japonicus* Bate 1888, demonstrated that copulation takes place in a head to head position, the sternum of the male pressing against that of the female. Previously, Burkenroad (1934) and later King (1948) presented hypotheses concerning the transfer of the spermatophores to the thelycum, taking into account the probable utilization of the petasma—apparently so well fitted to lodge the compound spermatophore—and the pereopods. No satisfactory explanation, however, has been advanced as to how a rotation of the spermatophore through 180° around its longitudinal axis, is accomplished.

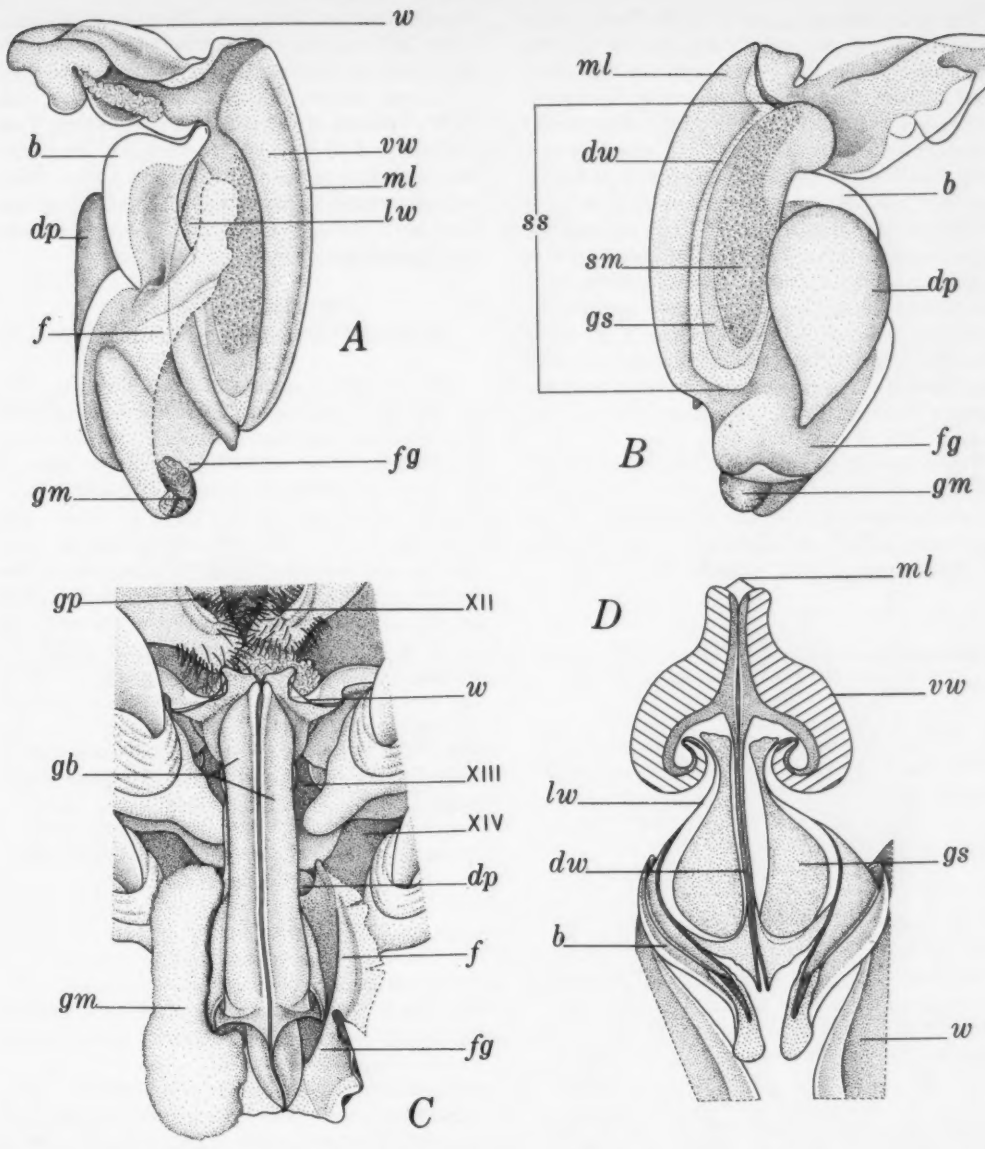

FIGURE 1.—The spermatophores of *Penaeus* (*Litopenaeus*) *schmitti* and *P.* (*L.*) *setiferus* illustrating terms used in the descriptive accounts. *A*, Ventrolateral view of *P.* (*L.*) *schmitti*. *B*, Dorsomesial view of same. *C*, Ventral view of a compound spermatophore of *P.* (*L.*) *setiferus* attached to female. *D*, Cross section of the geminate body of same, immediately posterior to the wings (in preparation of the section the blades together with the torn contiguous portion of the lateral walls have become displaced laterally). *b*, blade; *dp*, dorsal plate; *dw*, dorsomesial wall; *f*, flap; *fg*, flange; *gb*, geminate body; *gm*, glutinous material; *gp*, gonopore; *gs*, gelatinous substance; *lw*, lateral wall; *ml*, mesial lapel; *sm*, sperm mass; *ss*, sperm sac; *vw*, ventral wall; *w*, wing; XII, XIII, and XIV, sternites.

The intent of this paper is to present detailed descriptions of the spermatophores of the five species of *Litopenaeus*. Except for the close resemblance of the spermatophores of *P. schmitti* and *P. setiferus*, all of them, although structurally similar, are quite different in appearance; therefore I have emphasized apparent homologies. An effort has been made to explain the manner in which the spermatozoa egress from the spermatophores to fertilize the eggs. The association of the components of attached spermatophores with the corresponding thelycum in each species is indicated. Finally, the role played by the coxal plates of the third through the fifth pairs of pereopods of the females in keeping the compound spermatophore attached to the thelycum is briefly discussed.

The material examined is indicated in the treatment of each species. The following abbreviations are used for repositories of the specimens: ANSP - Academy of Natural Sciences of Philadelphia; INIBP - Instituto Nacional de Investigaciones Biológico-Pesqueras, México; UNC-IMS - Institute of Marine Sciences, University of North Carolina; USNM - National Museum of Natural History, Smithsonian Institution; and YPM - Peabody Museum of Natural History, Yale University. The carapace length (cl) is the linear distance between the orbital margin and the mid-posterior margin of the carapace. The illustrations have been made from preserved specimens; the accompanying scales are in millimeters.

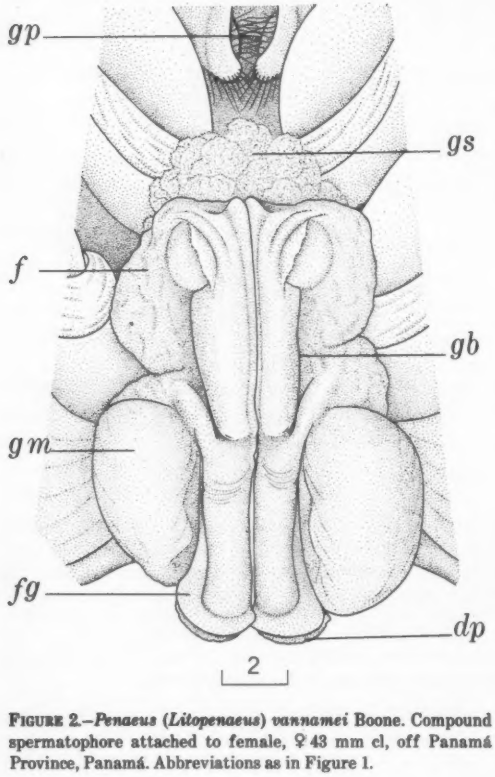

FIGURE 2.—*Penaeus* (*Litopenaeus*) *vannamei* Boone. Compound spermatophore attached to female, ♀ 43 mm cl, off Panamá Province, Panamá. Abbreviations as in Figure 1.

DESCRIPTIONS OF SPERMATOPHORES AND THELYCA

The descriptive accounts of the Pacific species are ordered according to the relative complexity of the respective spermatophores (*P. vannamei*, *P. occidentalis*, and *P. stylirostris*), and are followed by those of the Atlantic species (*P. schmitti* and *P. setiferus*), the spermatophores of which are markedly similar. The spermatophores of each species are described both as attached to the females, where they invariably occur in pairs, and as they appear when removed from the terminal ampullae of males. Next, detailed accounts of the thelyca are presented, which emphasize the main features for the support of the component parts of the spermatophores. A list of the material examined is given, including the numbers of impregnated females. Finally, the geographic range of each species is indicated.

Penaeus (*Litopenaeus*) *vannamei* Boone 1931
Figures 2-4

Spermatophore

The compound spermatophore (Figure 2) consists of a slender geminate body lacking wings and blades, and bearing thick, broad, lateral flaps, and a pair of long, caudal flanges.

Ventrally, each spermatophore (Figure 3A) exhibits a lateral furrow that roughly delimits a subovate anterior portion, bulging laterally, from an elongate, smoothly convex portion that extends to the flange; the thick, opaque ventral wall merges indistinctly with the lateral wall, which is mostly opaque and to which is loosely attached a conspicuous internal lamina; posteriorly, just before joining the flange, these walls turn strongly dorsad along an oblique line forming the fundus of the sac. The broad, mantlelike flap projecting from the lateral wall is thick, fleshy ventrally, and

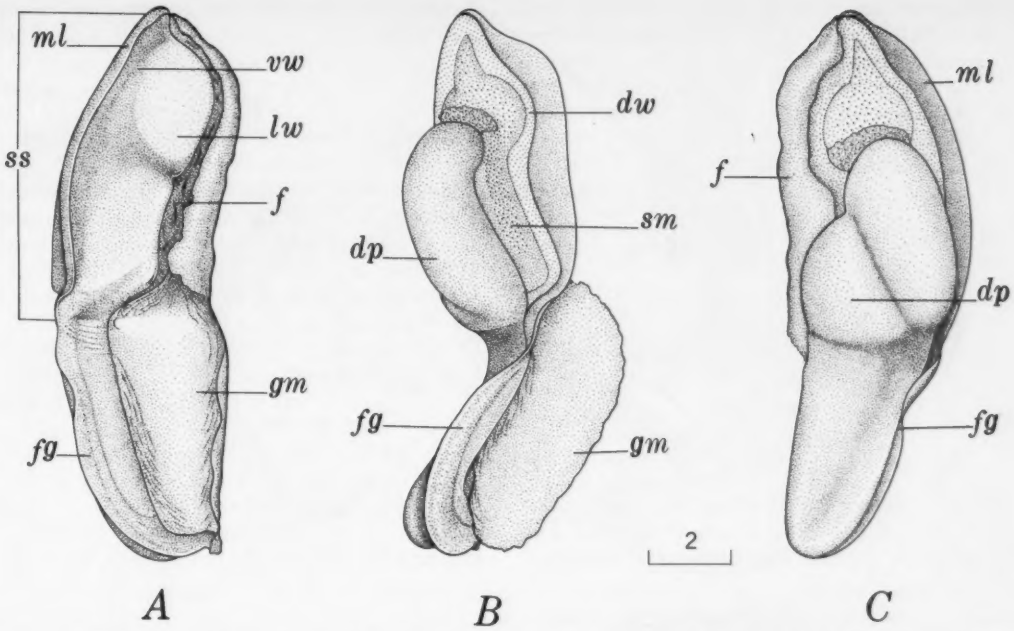

FIGURE 3.—*Penaeus* (*Litopenaeus*) *vannamei*. Left spermatophore dissected from terminal ampulla, ♂ off Juan Díaz, Panamá. *A*, Ventrolateral view. *B*, Mesial view. *C*, Dorsolateral view (glutinous material removed). Abbreviations as in Figure 1.

narrows anteromesially along the border of the sac; posteriorly along the flange, it continues as a flexible, but rather tough, narrow band. The flange is long, directed caudally, with the anterior portion marked by transverse wrinkles; a convex ridge runs parallel and contiguous to the free mesial margin along most of the entire length of the flange, and its lateral margin bears the narrow band from which a voluminous glutinous material is suspended. The thin but rigid dorsomesial wall (Figure 3B) is very broad basally and tapers anteriorly where it is produced in a subconical hood.

The dorsal plate is long (Figure 3C), the longest in the spermatophores of the five species, and at the base of the flange is bent strongly dorsally, the concavity thus formed delimiting two distinct parts. The anterior part, firmly attached to the dorsomesial wall, is nearly triangular in outline and elevated in a blunt mesial ridge which terminates anteriorly in a convex border at about the level of the lateral furrow; the posterior part is mostly flattened, and extends over the flange reaching, or almost reaching, its posterior margin.

The sperm mass, together with the gelatinous substance, is concentrated anteriorly in a large subspherical protuberance filling the lateral bulge and extends as a column in the posterior portion of the sac.

Thelycum (Figure 4A, B)

Sternite XIV bears a pair of setose, sigmoid, obliquely oriented anterolateral ridges, the lateral portions of which are low and rounded and the posteromesial portions high and sharp; the latter are continuous caudally with short elevations flanking a shallow central depression; sculpture is lacking on the posterior part of the sternite. Extending ventrally from the platelike posterior part of sternite XIII is a large, inverted, troughlike median protuberance which forms the anterior wall of a concavity bounded posteriorly by ridges of sternite XIV; the posterior part of the sternite XIII is also provided with a pair of small teeth, subjacent to the base of the median protuberance, and a pair of hornlike marginal projections lateral to the protuberance. The anterior part of sternite XIII bears two small setose lateral prominences, located close to the margin which is overhung

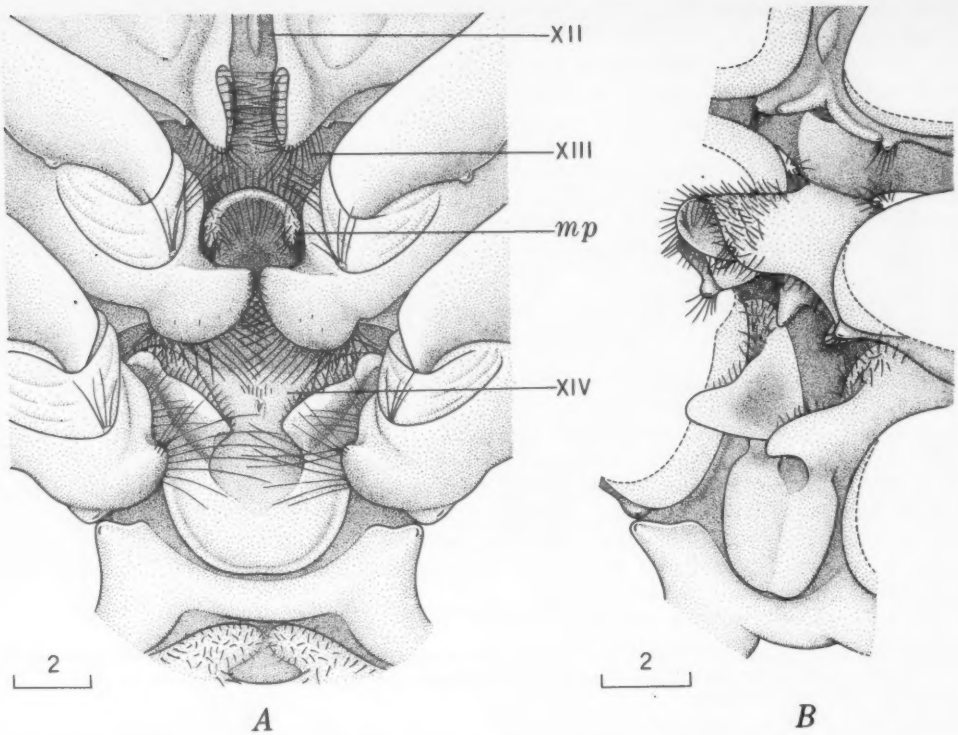

FIGURE 4.—*Penaeus* (*Litopenaeus*) *vannamei*. *A*, Thelycum, ♀51 mm cl, NW Península de Azuero, Panamá. B, Ventrolateral view of thelycum, ♀48 mm cl, same locality, *mp*, median protuberance; XII, XIII, and XIV, sternites.

ventrally by the short posteromesial extensions (protecting the gonopores) of the coxae of the third pereopods.

Disposition of the Compound Spermatophore on the Thelycum

When attached to the female, the compound spermatophore forms a distinct arc, the fundus of the sperm sacs being elevated (ventrally) well above the sternum. The sacs are thus directed anterodorsally with the anteriormost portions of their ventral walls resting on the border of the median protuberance of sternite XIII, and the contiguous lateral flaps extending over the coxae of the fourth pereopods; these flaps seem to serve as stabilizers for the rather compressed, vertically extended sacs. Anteriorly, the bulges of the sacs become very conspicuous, and the practically fused dorsomesial walls lie almost perpendicular to the horizontal coxal plates of the fourth pereopods. The sperm is released at the level of the median protuberance of the female, thus not as close to the gonopores as in the remaining species of the group. In opposition to the paired sacs, the flanges are directed posterodorsally reaching the first pleonic sternite; they cover the dorsal plates ventrally, embrace them mesially, and are flanked laterally by the glutinous material suspended from their narrow flaps. The anterior parts of the dorsal plates, which seem to be the principal elements of attachment of the spermatophores in this species, become fused along their mesial ridges, and are basally affixed to sternite XIV (pressing against the thelycal ridges) as well as to the coxae of the fifth pereopods. The posterior parts of the dorsal plates, in turn, lie on the transverse setose patch of the first pleonic sternite. Finally, the gelatinous substance, protruding through the anterodorsal extremity of the spermatophore, spreads over and beyond the thelycal protuberance of sternite XIII, while the paired

masses of glutinous material somewhat support the flanges.

Material

MEXICO. 6 ♂ 3 ♀, USNM, 6 km S of Bahía de Guaymas, Sonora, 23 November 1939, M. J. Lindner.- 10♂9♀, USNM, off San Simón, Chiapas, 24 m, I. Edén-Reyna.- 8♂3♀, INIBP, off Barra de Soconusco, Chiapas, 11 June 1960, F. Aguilar.

NICARAGUA. 2♂ 2♀, USNM, ex. Galveston Laboratory, National Marine Fisheries Service.

COSTA RICA. 1♀ [impregnated], USNM, off Parrita, 11 m, 8 March 1975, B. R. Drummond.- 4♀ [impregnated], USNM, off Dominical, 27 m, 8 March 1975, B. R. Drummond.

PANAMA. 18 ♂ 8♀, YPM, off Bella Vista, 8 February 1934, Bingham Oceanogr. Exped.- 2♂8♀, USNM, off Juan Díaz, 12 m, 16 February 1973, *Patricia*.- 2♂1♀,off Juan Díaz, 4 February 1969, L. G. Abele.- 4♂, USNM, off Juan Díaz, 8 m, 5 March 1973.- 4♀ [impregnated], USNM, off Panamá Prov., *Patricia*, 6 March 1973.- 1♀ [impregnated], Golfo de Panamá, ex. Instituto Nacional de Pesca de Panamá.- 3♀, USNM, NW Península de Azuero, 18 m, 14 December 1963, *Pelican* stn. 1614.

ECUADOR. 2♂ 1♀, USNM, Puerto Bolívar, 2 January 1964, Ortiz.

PERU. 2♀, USNM, Caleta Cruz, January 1969, E. M. del Solar.

Species Range

Gulf of California to Tumbes, Perú.

Penaeus (*Litopenaeus*) *occidentalis* Streets 1871
Figures 5-7

Spermatophore

The compound spermatophore is rather bizarre in appearance (Figure 5A, B), its geminate body bearing a pair of small anterolateral wings and a

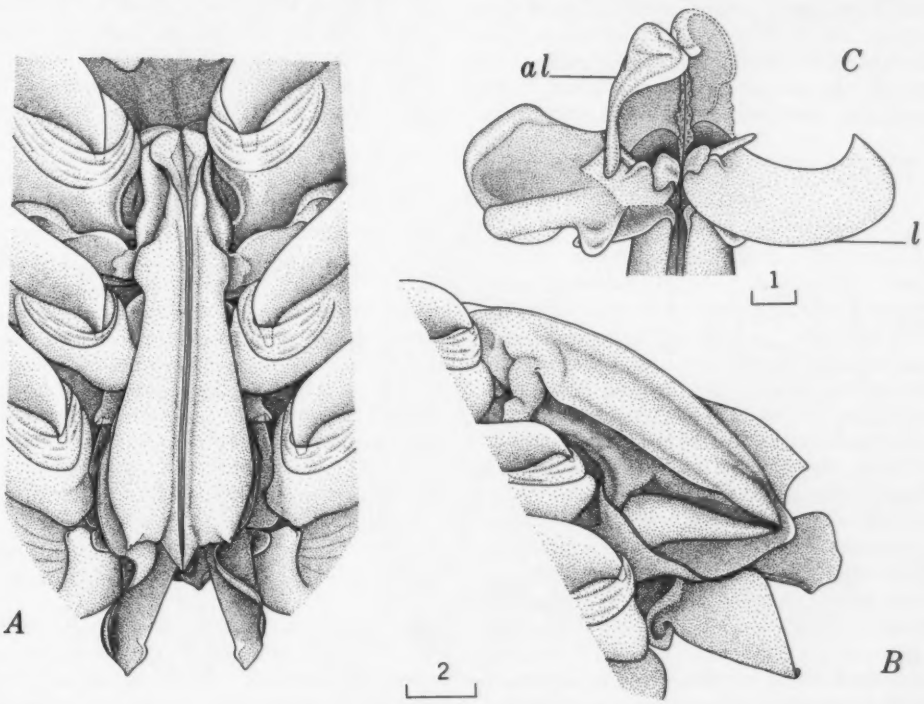

FIGURE 5.—*Penaeus* (*Litopenaeus*) *occidentalis* Streets. *A*, Compound spermatophore attached to female, ♀ 35.5 mm cl, off Panamá Province, Panamá. *B*, Lateral view of same specimen. *C*, Dorsal view of anterior part of compound spermatophore removed from female, ♀ 40 mm cl, same locality. *al*, anterior lobe; *l*, lamina.

pair of long, broad lateral blades; the posterior parts of the blades are continuous with rigid ventromesial extensions or flaps flanking the posterolateral portions of the geminate body, and terminate in large caudal lobes. The flanges, extremely short and extending caudolaterally, are hidden by the ventromesial extensions.

The thick ventral wall of each spermatophore broadens at the level of the wing and from there tapers anteriorly continuing as a bridge (marked by a dorsal concavity) joining a firm, fanlike anterior lobe (Figure 6A). This lobe is bordered anteromesially by a rib that is produced laterally in a small projection, and its lateral margin bears a shallow emargination which demarks two lateral convexities, the posterior one is hollow. The ventral wall and the thick caudal portion of the lateral wall join in an acute angle, and continue in a short, heavily sclerotized, caudal flange. A dorsolateral rib marks the junction of the mostly thin and translucent lateral wall with the dorsomesial wall, and serves as the base of the blade. The blade exhibits two lateral constrictions that mark three sections: the anterior one is broad, roughly subelliptical, and delimited posteriorly by a transverse rib; the median section, also broad, is subtrapezoidal, and the posterior one narrow and bends around the apex of the caudal lobe, finally turning mesially to join the posterior border of the flange. The caudal lobe is the rather flexible extremity of the rigid ventromesial extension projecting from the line along which the flange and corresponding blade meet. A narrow, iridescent membrane runs along the margin of the ventromesial extension, which sustains a glutinous material on its inner surface (the membrane is not represented in Figure 6A, D for the sake of clarity). The rigid and translucent dorsomesial wall (Figure 6B) completes the sperm sac, which terminates and opens anteriorly at the base of the anterior lobe, mesial to the base of the wing.

The small wing (Figure 6C) is roughly subelliptical in ventral view, but bears a proximodorsal lobular process and is produced distally and posteriorly in a ventrally turned fold continuous with a small shelf at the base of the process (Figure 5C). A rigid but fragile lamina (Figures 5C, 6A, B) lies at the base of, and perpendicular to the anterior lobe; it extends from the mesial part of the sperm sac laterally almost to the tip of the wing. This peculiar lamina bears on its mesial border two conspicuous projections with a small ridge between them; one of the projections is dorsally located, flattened and strongly curved

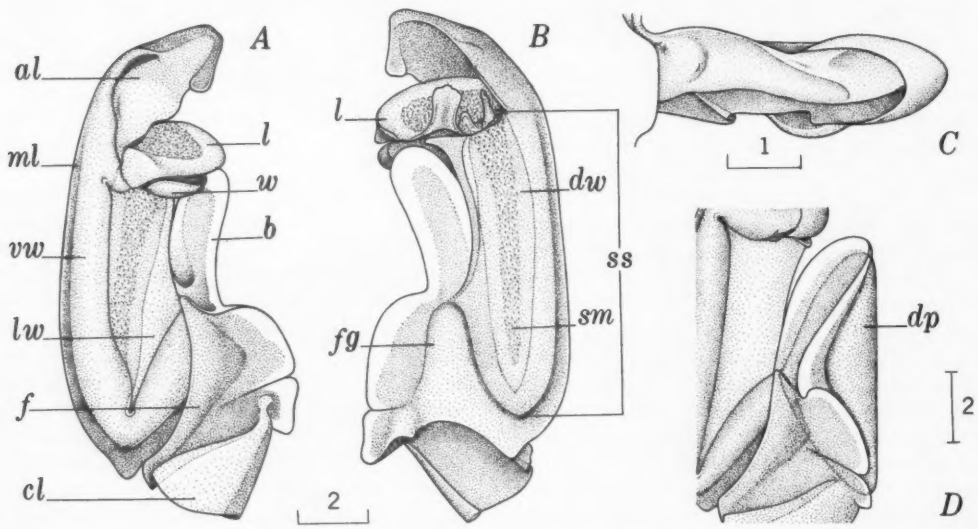

FIGURE 6.—*Penaeus* (*Litopenaeus*) *occidentalis*. *A*, Ventrolateral view of left spermatophore (dorsal plate removed) dissected from terminal ampulla, ♂ off Bella Vista, Panamá. *B*, Dorsomesial view of same specimen. *C*, Ventral view of wing as attached to female, ♀ 35.5 mm cl, off Panamá Province, Panamá. *D*, Lateral view of dorsal plate, ♂ off Punta Soldado, Buenaventura, Colombia. *al*, anterior lobe; *cl*, caudal lobe; *l*, lámina. Other abbreviations as in Figure 1.

laterally, whereas the other is spiniform—the tip of the latter projection shows in Figure 5A at the vertex of the emargination between anterior lobe and the base of wing.

The dorsal plate (Figure 6D) is almost as long as, and lies against the dorsal surface of the blade; it is produced in a central prominence that fits into the concavity on the posterior extremity of the anterior section of the blade.

Thelycum (Figure 7)

Sternite XIV is densely covered with setae except over a pair of posterolateral crescentic elevations separated by a short, sharp posteromedian ridge; this ridge is hidden in the adult by the bulging surrounding area. The posterior portions of the elevations are parallel to the thoracic ridge which typically bears a pair of lateral prominences provided with a brush of setae. Sternite XIII is heavily sclerotized posteriorly forming a plate with a broadly concave posteromedian margin not overlapping sternite XIV, but with lateral extremities produced into hornlike projections freely overhanging sternite XIV. The central region of the plate bears a strong rounded to subconical knob and the posterior margin occasionally is armed with a small median tooth. The anterior part of sternite XIII is provided with a pair of transverse folds, the mesial portions of which are produced into sharply pointed conical projections covered by minute setae. The strong posterior ridge of sternite XII is divided by a median depression, and its lateral extremities are produced caudally in a pair of convexities hidden by the scooplike coxal plates of the third pereopods. These uniquely shaped coxal plates support the sperm sacs anteriorly and seem to retain, at least briefly, the sperm masses immediately after their release. It should be remembered that the coxal plates are covered ventrally by the bases of the anterior lobes of the spermatophores.

Disposition of the Compound Spermatophore on the Thelycum

When the compound spermatophore is in position on the female, the fanlike anterior lobes become affixed to sternite XII with the lateral portions lying beneath the coxae of the third pereopods while their basal portions extend over (ventrally) the coxal plates. The angular junctions between the anterior lobes and the wings embrace

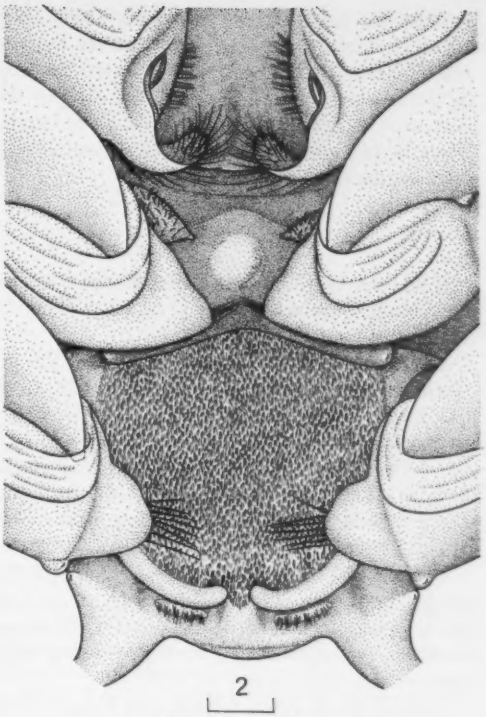

FIGURE 7.—*Penaeus* (*Litopenaeus*) *occidentalis*. Thelycum, ♀53.5 mm, cl, Golfo de Panamá, Panamá.

the posterior extremity of the corresponding female gonopore. The mesial borders of the laminae, in turn, form supporting rims along the lateral borders of the apertures of the respective sperm sacs, and the flattened projections of the laminae meet in the sagittal plane, while the spiniform projections lie contiguous to the posterior convexities of the anterior lobes (Figure 5C). The laminae extend laterally, adhering to the posteroventral surface of the coxae of the third pereopods, and the wings rest ventrally over and against the laminae, both processes helping to anchor the spermatophores to the thelycum. The position assumed by the anterior part of the spermatophore on the female brings the apertures of the sperm sacs to the coxal plates of the third pereopods and thus close to the gonopores; consequently, it seems that the sperm might well accumulate on these spoonlike coxal plates. Whether or not the opening of each sac is permanent, or results from a rupture, has not been ascertained.

Posterior to the wings, the lateral blades press

against the subjacent dorsal plates which come together, meeting mesially, and adhere to sternites XIII and XIV. The narrow posterior portions of the blades meet on the midline, forcing the geminate body ventrally and causing the caudal lobes to project posteroventrally, resembling paired rudders.

Material

MEXICO. 1♀, USNM, between Monte Alto and San José, Chiapas, 25 m, 8 August 1970, D. Palacios.

PANAMA. 6 ♂ 2♀, syntypes, ANSP No. 73, "Isthmus of Panama," J. A. McNeil.- 6♂ 12♀, YPM, off Bella Vista, 9 February 1934, Bingham Oceanogr. Exped.- 7♂, USNM, off Juan Díaz, 4.5-7 m, 26 February 1973, *Patricia*.-2♀ [impregnated], USNM, off Panamá Prov., 6 March 1973, *Patricia*.- 1♂ 1♀, USNM, E of Panamá City, 7 m, 5 November 1971, D. E. Sweat.

COLOMBIA. 12♂ 12♀ [1♀ impregnated], USNM, off Punta Soldado, Buenaventura, 4.5 m, 1 March 1973, *Santanderino*.- 6 ♂ 13 ♀, USNM, Tortugas Grounds, Buenaventura, 9 m, 19 September 1969, *Cacique* stn. 69-24.

ECUADOR. 6 ♂ 3♀, USNM, off Playas, 1963, commercial catches.

PERU. 1♀, USNM, Caleta Cruz, Tumbes, 18 m, January 1969, E. M. del Solar.

Species Range

Chiapas, México, to Tumbes, Perú, and Islas Galápagos.

Penaeus (*Litopenaeus*) *stylirostris* Stimpson 1871 Figures 8-12

Spermatophore

The compound spermatophore consists of a slender, geminate body produced into large anterolateral wings, broad posterolateral flanges, and bearing paired elongate blades (Figure 8).

The ventral wall of each spermatophore is truncate anteriorly; posteriorly it continues indistinctly with the thick posterior portion of the lateral wall, both walls then turning abruptly dorsad forming the fundus of the sac just before joining the flange (Figure 9A). The lateral wall, mostly thin, is bounded by a very fine dorsolateral rib. This rib serves as the base of a long, moderately broad blade, which extends from the base of the wing (there fused to its posterior ridge) to the anterior extremity of the flange, and continues along the entire border of the latter. The blade is somewhat arched over its attachment to the rib, which delimits two longitudinal parts. One part is directed dorsomesially to the base of the flange, where it twists laterally, the other part projects ventromesially throughout its entire length, and bears anteriorly an iridescent, rather membranous broad flap to which adheres (dorsally) a mass of viscous material; along the flange the ventromesially projecting part becomes flexible and sustains a narrow extension of the flap, supporting a mass of glutinous material on its mesial surface. The flange is somewhat broadly ovate, and is covered by a large dorsal plate which occupies its entire surface and extends beyond the flange

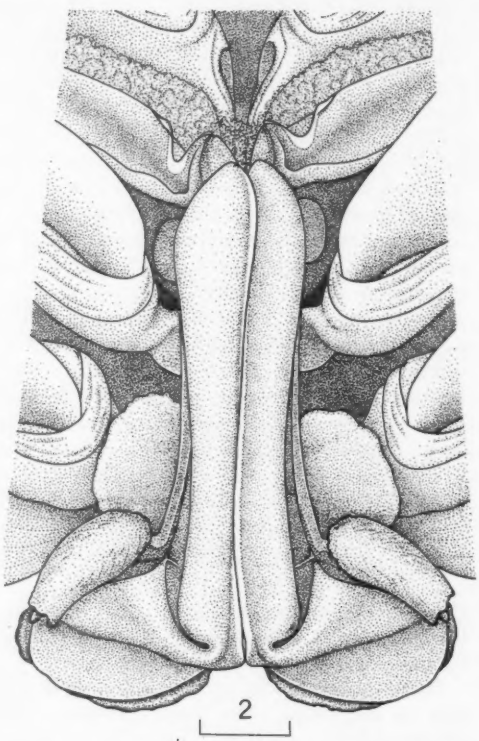

FIGURE 8.—*Penaeus* (*Litopenaeus*) *stylirostris* Stimpson. Compound spermatophore attached to female (geminate body slightly displaced posteriorly to show bases of wings), ♀38 mm cl, off Panamá Province, Panamá.

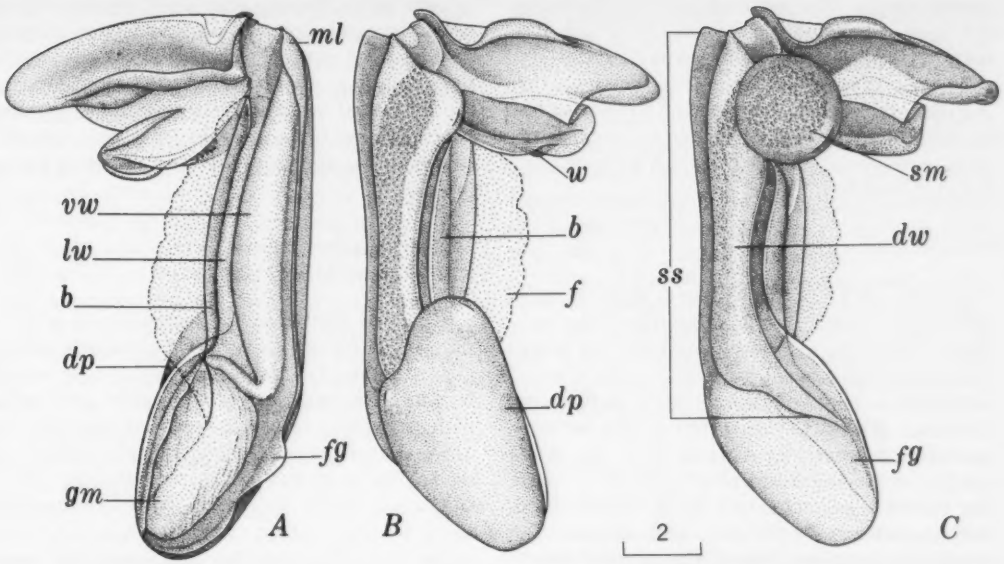

FIGURE 9.—*Penaeus* (*Litopenaeus*) *stylirostris*. *A*, Ventrolateral view of right spermatophore dissected from terminal ampulla, ♂ off Juan Díaz, Panamá. *B*, Dorsomesial view of same specimen. *C*, Dorsomesial view of right spermatophore forcefully expelled from terminal ampulla, ♂ off Panamá Province, Panamá. (For the purpose of illustration the anterior ventromesially directed part of the blade has been turned laterally and the viscous material removed.) Abbreviations as in Figure 1.

anteriorly in a rounded portion affixed to the dorsomesial wall.

In this spermatophore, the dorsomesial wall (Figure 9B, C) is turned upon itself and attached to the mesial lapel of the ventral wall, but not joining the lateral wall—except posteriorly, where they become fused. Consequently, the lateral wall and part of the ventral wall overlap the sac (largely formed by the dorsomesial wall) as a protecting shield. The sac is subconical anteriorly; it expands in a conspicuous rounded bulge at the base of the wing, and continues into the elongate posterior portion affixed to the base of the flange and firmly attached to the dorsal plate.

The wing (Figure 10A, B) consists of a transversely elongate, mostly sclerotized anterior region, and a subrectangular, membranous posterior region. The anterior region bears a long, sharp, ventral ridge, joining a short, pointed, basal rib at almost a 90° angle; the area laterally contiguous to the basal rib is membranous, whereas that mesial to it is thick, but soft, and meets the ventral wall of the sac. Dorsally, the wing is produced in a broad, rounded lobe, situated close to its anteroproximal margin. The membranous region of the wing bears a posterior rib that ends

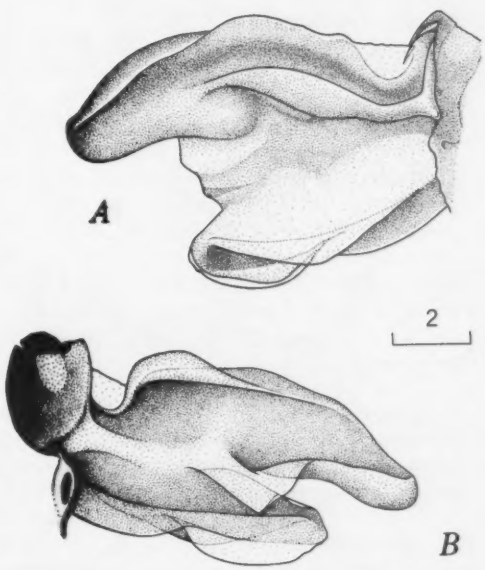

FIGURE 10.—*Penaeus* (*Litopenaeus*) *stylirostris*. Wing severed from geminate body of right spermatophore, ♂ off Playas, Ecuador. *A*, Ventral view, posterior membranous region extended. *B*, Dorsal view of same specimen.

premarginally. The posterolateral membranous extension is reflexed and attached to the rib dorsally, thus forming a shallow pocket. After the compound spermatophore is deposited on the thelycum, the pockets of the paired wings come to lie posteromesially and are quite conspicuous on those impregnated females in which the geminate body has been lost.

Thelycum (Figure 11)

Sternite XIV bears a large median subpyramidal prominence with a subtriangular base (broad anteriorly, tapering posteriorly), its sharp midlongitudinal carina armed with a row of very minute setae. The highly sclerotized posterior part of sternite XIII is produced into a rigid, subvertical shelf overhanging sternite XIV; this shelf constitutes the posterior wall of a pair of concavities which are separated by a sharp median ridge and are delimited anteriorly and laterally by strong angular paired ridges, the posterior bases of which extend laterally and bear toothlike projections. The anterolateral part of sternite XIII bears paired transverse rigid elevations covered by long setae. Heavily sclerotized sternite XII is nearly straight along its posteromedian margin, and produced caudally in a pair of lateral projections armed with tufts of setae. The conspicuous concavities of sternite XIII serve to lodge the sperm masses which emerge from the ruptured anterodorsal bulges of the compound spermatophore.

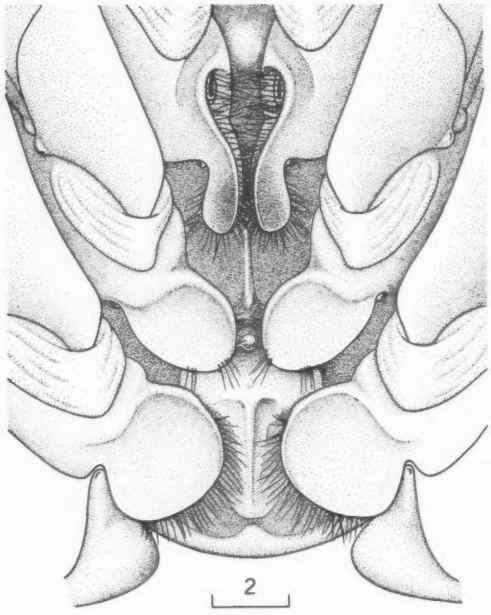

FIGURE 11.—*Penaeus* (*Litopenaeus*) *stylirostris*. Thelycum, ♀46 mm cl, off Bella Vista, Panamá.

Disposition of the Compound Spermatophore on the Thelycum

When the compound spermatophore is in position on the female, the anterior extremity of the geminate body lies on the ventrally turned mesial borders of the coxal plates of the third pereopods, with the sperm masses (projecting through the anterodorsal bulges) lodged in paired thelycal concavities of sternite XIII, near the gonopores (Figure 12). The wings contribute to anchoring the spermatophore: their anterior regions are attached to the posteroventral surfaces of the coxae of the third pereopods, the mesial portions following the contour of the strongly curved coxal plates; lobes borne on the dorsal side of the anterior regions certainly function as adhesive elements. The posterior region of each wing is extended

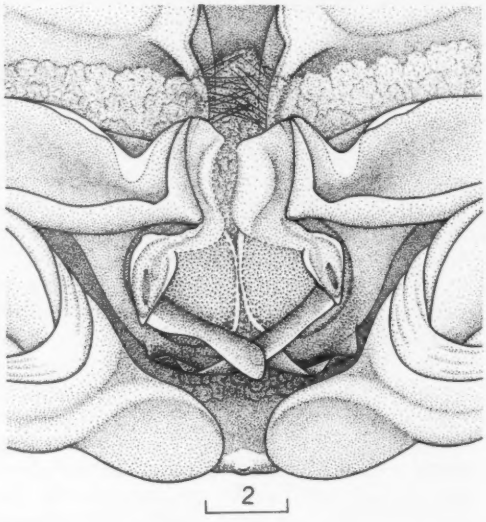

FIGURE 12.—*Penaeus* (*Litopenaeus*) *stylirostris*. Sternites XII and XIII bearing paired masses of sperm and wings of a compound spermatophore, the geminate body of which has been lost (see explanation in text), ♀48 mm cl, off Guaymas, México.

mesially, each with its marginal rib embracing the sperm mass protruding through the corresponding sac; the adjacent membranous portions cover each mass laterally and from there extend tightly attached to sternite XIII.

From the bases of the wings posteriorly, the lateral portions of the ventral walls together with the lateral walls are turned mesially in a spiral thus reducing the lumen of the sacs; at the same time, each blade comes to occupy a position deep within a fold so that the dorsomesial part of the blade abuts against the respective sac, and the other part, together with its flap, projects somewhat laterally. Caudally, the geminate body reaches the first pleonic sternite, and the thick portions of the lateral walls are turned sharply anterolaterad resulting in the elevation of paired ridges. These are continuous with the flanges which posteriorly extend laterally from the geminate body and either embrace or enfold the dorsal plates. These plates are attached in such a way that their smaller anterior parts rest against the coxal plates of the fifth pereopods, and their broad posterior parts (extending across the corresponding flange) lie almost entirely on the first pleonic sternite. Finally, the glutinous material, resting along the anterior borders of the flanges, become almost perpendicular to the median body.

As the compound spermatophore is anchored to the female, gelatinous substance extends over the coxae of the third pereopods and under the wings, penetrates the area between the coxal plates of those pereopods and covers the posterior portion of sternite XII.

In *Penaeus stylirostris* the spermatozoa are apparently released by the rupture of the attached spermatophore. By some unknown means, the geminate body with adjoining flanges breaks away, leaving the wings, together with paired rounded masses of sperm surrounded by gelatinous substance, on the female. It seems that when the spermatophores are expelled, the spermatozoa and the gelatinous substance, which were previously within the sacs, are forced into, and then break through, the anterolateral bulges, finally becoming lodged in the thelycal concavities of sternite XIII. In the extruded spermatophores that I have examined—removed from impregnated females or obtained by forcing their expulsion from the terminal ampullae of males—the sacs retained but little sperm. The wings are torn from the geminate body along the line of union between their mesial extensions and the corresponding ventral wall, and the break continues across the lateral wall to the posterior ridge of the respective wing. The rupture does not occur along definite sutures, but it follows the pattern described. Once the geminate body breaks away, the spermatozoa are exposed to the surrounding water, in close proximity to the female gonopores.

On one of the females examined there was an entire spermatophore superimposed upon the remains of another, the latter represented by a pair of wings and remnants of a sperm mass. This indicates that the animal had copulated twice within a short period of time.

Material

MEXICO. 1 ♂ 2 ♀ [impregnated], USNM, off Guaymas, Sonora, 8 April 1940, Capt. Corona.- 2 ♀ [impregnated], USNM, off Guaymas, Sonora, 9 April 1940, E. F. Ricketts.- 2 ♂ 2 ♀, INIBP, Bahía de Altata, Sinaloa, 14 April 1959, commercial catches.- 4 ♂ 3 ♀, USNM, between Monte Alto and San José, Chiapas, 25 m, 8 August 1970, D. Palacios.

COSTA RICA. 3 ♀ [impregnated], USNM, Parrita, SE of Puntarenas, 27 m, 4 July 1974, B. R. Drummond.- 1 ♀ [impregnated], USNM, off Parrita, 11 m, 8 March 1975, B. R. Drummond. 2 ♀ [impregnated], USNM, off Parrita, 18 m, 8 March 1975, B. R. Drummond. 5 ♀, [impregnated], USNM, off mouth Río Coronado, 16 m, 10 March 1975, *María del Pilar*.

PANAMA. 4 ♂ 9 ♀, USNM, off Panamá Prov., 12-24 m, 16 February 1973, *Patricia*.- 14 ♂ 1 ♀, USNM, 4.5-7.5 m, of Juan Díaz, 26 February 1973.- 6 ♂, USNM, off Panamá Prov., 5 March 1973.- 4 ♀ [impregnated], USNM, off Panamá Prov., 6 March 1973, *Patricia*.- 1 ♂ 3 ♀, USNM, Isla Gorgona, 1 m, March 1973, fishermen.

ECUADOR. 1 ♂ 1 ♀, USNM, off Playas, 3 December 1963, San Andrés.- 1 ♂, USNM, Ensenada de Valdivia, December 1934, S. Camino.

PERU. 2 ♂ 2 ♀, USNM, off Puerto Pizarro, 11 May 1941.

Species Range

Punta Abreojos, Territorio de Baja California, and Gulf of California, México, to Tumbes, Perú.

Penaeus (*Litopenaeus*) *schmitti* Burkenroad 1936 Figures 1A, B, 13-15

Spermatophore

The compound spermatophore consists of a geminate body produced in a pair of anterolateral wings, flanked caudolaterally by flanges broadened posteriorly and bearing wide lateral flaps (Figure 13A, B).

Anteriorly, the thick, opaque ventral wall of each spermatophore is truncate and strongly inclined dorsally (Figure 14A); posteriorly, it is imperceptibly continuous with the thick portion of the lateral wall, both turning abruptly dorsad forming the fundus of the sac. The lateral wall bears a small, blunt to acute caudal projection, just before joining the flange. The flange is narrow and horizontal anteriorly, it becomes progressively broader posteriorly, and turning mesially is deflected ventrally becoming almost perpendicular to its anterior portion. The lateral wall is bounded dorsolaterally by a fine rib that serves as base for the anterior part of a long blade. The blade is divided by a deep horizontal incision. The anterior part is narrow and convex at its cephalic extremity, then broadens abruptly and reaches the flange where its free caudal margin overhangs (ventrally) the cephalic margin of the posterior part. The posterior part, in turn, is narrow and runs along the lateral border of the flange, tapering caudally. The flange bears a broad, lateral flap which is produced anteriorly in a narrow strip running laterally along the sac; the broad portion of the flap is strengthened by a subtriangular

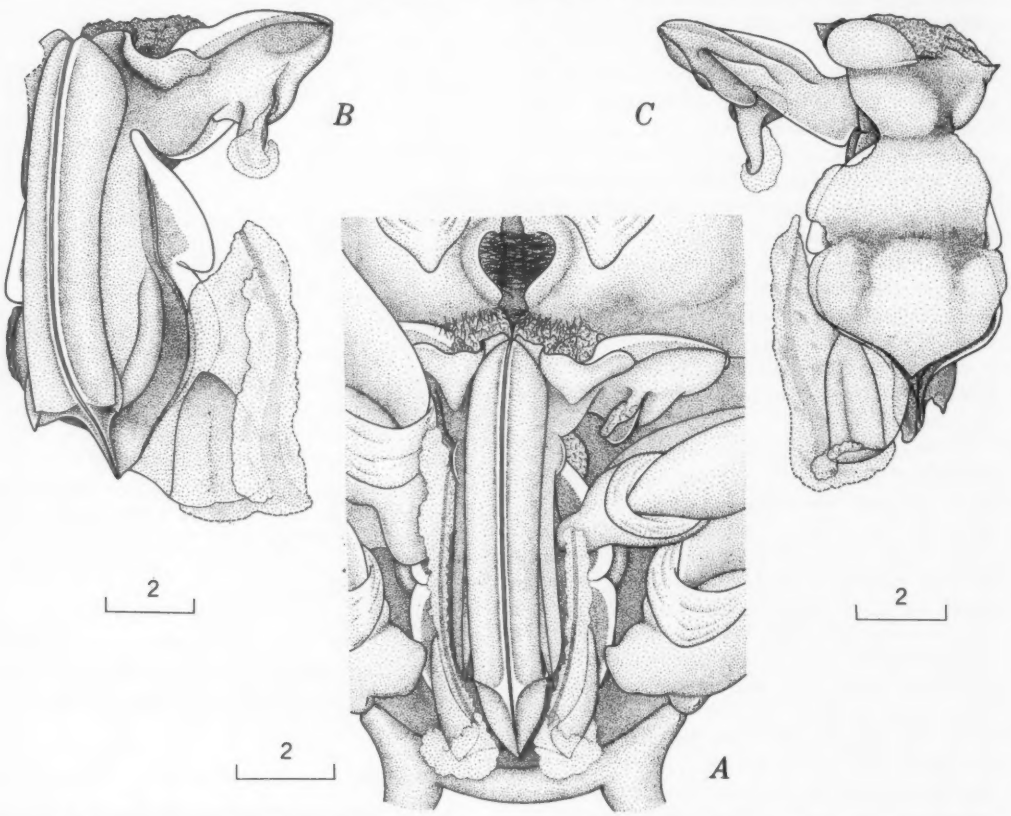

FIGURE 13.—*Penaeus* (*Litopenaeus*) *schmitti* Burkenroad. *A*, Compound spermatophore attached to female, ♀ 34 mm cl, off Tucuracas, Península de la Guajira, Colombia. *B*, Ventrolateral view of compound spermatophore dislodged from female, ♀ off Honduras. *C*, Dorsal view of same specimen (anterodorsal extremity missing).

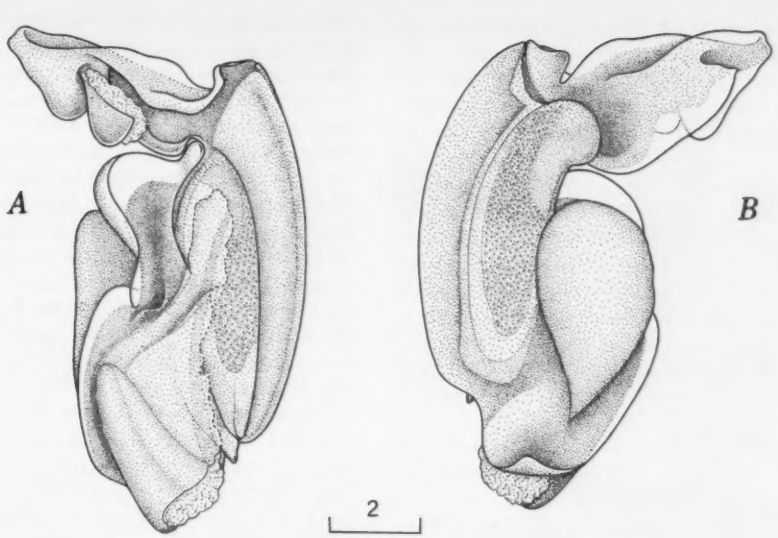

FIGURE 14.—*Penaeus* (*Litopenaeus*) *schmitti*. *A*, Ventrolateral view of right spermatophore dissected from terminal ampulla, ♂ off Ubatuba, São Paulo, Brasil, *B*, Dorsomesial view of same specimen.

plate and a submarginal thickness somewhat stiffens the entire flap. A glutinous material rests against the flange, and adheres to the mesial surface of the flap.

The thin, translucent dorsomesial wall bulges conspicuously beyond its attachment along an oblique line extending from the anterior extremity of the mesial lapel to the posteroproximal end of the wing (Figure 14B; this bulge, occupied by the extremity of the sperm mass enclosed in the spermatophore, bears a triangular crest, rather similar to the subconical anterior extremity of the sperm sac in *P. stylirostris*. Posterior to the bulge, the dorsomesial wall, as in all the other spermatophores, is attached to the mesial lapel along its entire length, extending laterally to join the blade, and caudally to become affixed to the base of the flange.

The wing is long and irregular in contour, produced caudally in a broad proximal lobe, and tapers to a rounded excavated tip. The ventral surface is scabrous, bearing several projections: a rigid, rounded prominence on the anterior rib; an elongate, twisted process (its base situated slightly distal to midlength) that extends mesially in the form of a subovate to nearly semicircular lobule; and a distal shelf, obliquely flanking the process posterolaterally.

The dorsal plate (Figure 14B) is roughly tear-shaped, rounded anteriorly, tapering posteriorly, and relatively long, extending from the anterior end of the blade (at the base of the wing) almost to its posterior tip. The plate is intimately associated with the blade anteriorly, and practically fused to the flange posteriorly.

Thelycum (Figure 15)

Sternite XIV bears a pair of subparallel anterolateral ridges which extend posteriorly without turning mesially, to reach two rigid rounded or subconical prominences; a narrow median sulcus often divided by a slender longitudinal rib is present anterior to the prominences. Sternite XIII is rigidly sclerotized forming a strong plate produced posteriorly as an emarginate soft shelf overhanging sternite XIV; the anterior part of this sternite bears a pair of soft and naked transverse elevations flanking a tonguelike lamella bordered by setae. The lamella forms the roof of a concavity floored by a strong ridge from sternite XII. The ridge (a marginal thickening of platelike sternite XII and mostly hidden by setose, rounded, and relatively short coxal plates of the third pereopods) is produced into two pairs of convex projections, a small median pair and considerably larger lateral ones armed with long setae. The concavity of sternite

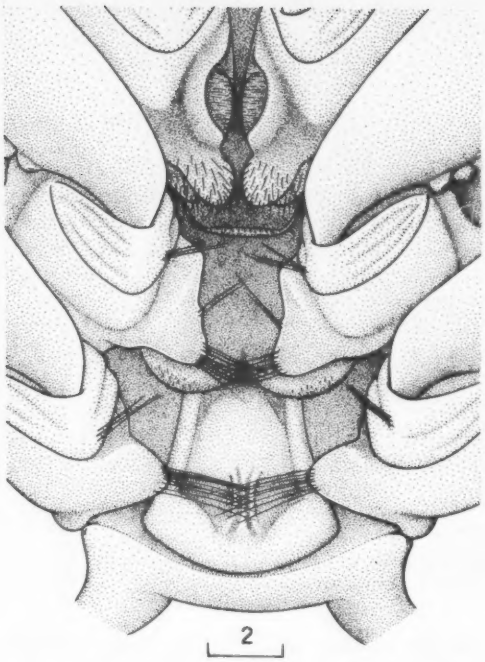

FIGURE 15.—*Penaeus* (*Litopenaeus*) *schmitti*. Thelycum, ♀50 mm cl, off Paramaribo, Surinam.

XIII serves to receive the sperm masses projecting through the ruptured anterodorsal bulges of the compound spermatophore, a function similar to that of paired concavities present on the same sternite in *P. stylirostris*.

Disposition of the Compound Spermatophore on the Thelycum

At mating, the compound spermatophore is applied to the thelycum with the anterior part of the geminate body lying on the mesial margins of the coxal plates of the third pereopods, in close proximity to the gonopores (Figure 13A). Basally, the wings extend over (ventrally) the coxal plates, their posterior lobes embrace laterally the sperm masses emerging from the sacs, and are attached caudal to the tonguelike lamella of sternite XIII, where they are almost contiguous; the anteromesial margins of the wings, however, are free, leaving a passageway between them and the body of the female, through which protrudes gelatinous substance. The wings are affixed distally to sternite XIII, with the twisted processes turned strongly posteromesiad and hidden by the articular (dorsal) membranes of the corresponding fourth pereopod. The sperm masses which emerge through the ruptured anterodorsal bulges of the spermatophore are lodged within the concavity roofed by the lamella of sternite XIII and floored by the strong ridge projecting from sternite XII. The sperm-filled concavity is lined by the gelatinous substance which surrounded the sperm while in the sac. Caudally, the geminate body extends to the posterior part of sternite XIV, where the posteromesial portions of the flanges meet on the sagittal plane and form a vertical shelf that is situated between the two thelycal protuberances. The broad anterior parts of the paired blades and the lateral (anterior) portions of the flanges are attached to sternite XIII and XIV successively, pressing against the dorsal plates. The broad flaps borne by the flanges conspicuously flank the geminate body, and the glutinous material—adhering to their mesial surfaces—enlarge, extending along the sides of the geminate body. The dorsal plates fuse in a single mass which is directly applied to sternites XIII and XIV, and which anteriorly abuts the indurate gelatinous substance enveloping the sperm masses within the concavity of sternite XIII (Figure 13C).

Several years ago, during the course of field work in Caribbean waters, I examined a few females carrying complete spermatophores as well as a few others bearing only those elements of the spermatophores which become affixed to sternite XIII. The latter specimens indicate that after the compound spermatophore is attached to the female, the geminate body is severed leaving behind only the wings and paired masses of sperm. Remarks on the rupture of the spermatophore in *P. setiferus*, which occurs in about the same manner as it does in *P. schmitti*, are presented on p. 481.

Material

Many specimens examined by me are recorded in Pérez Farfante (1969). Two females with spermatophores attached studied during the course of this investigation are in the lots listed below.

COLOMBIA. 6 ♂ 10♀, USNM, off Tucuracas, Península de la Guajira, 22 m, 6 October 1965, *Oregon* stn. 5674.

SURINAM. 1♀, USNM, E of Braams Point, 22 m, 30 May 1957, *Coquette* stn. 155.

A complete spermatophore dislodged from a female caught off Honduras was also examined. It is deposited in the USNM, and was presented by Eric J. Heald.

Species Range

Cuba to Guadeloupe, and along the continental coast from Belize (British Honduras) to Laguna, Santa Catarina.

Penaeus (*Litopenaeus*) *setiferus* (Linnaeus 1767) Figures 1C, D, 16-19

Spermatophore

The compound spermatophore consists of a geminate body which bears a pair of anterolateral wings, and is flanked posterolaterally by a pair of flanges which broaden posteriorly and bear broad flaps (Figure 16A, B).

Anteriorly, the thick, opaque ventral wall of each spermatophore is truncate and strongly inclined dorsally (Figure 17A); posteriorly, it turns abruptly dorsad, and merges indistinctly with the thick posterior portion of the lateral wall, which bears a small, acute or blunt caudal projection. The thin and translucent portion of the lateral wall is bounded dorsolaterally by a rib that serves as a base for the narrow, scalloped blade which extends caudally along the lateral margin of the flange. The flange is narrow and horizontal anteriorly, becomes progressively broad posteriorly, and turning mesially is deflected ventrally becoming almost perpendicular to its anterior portion. Laterally, the flange sustains a broad, ventromesially directed firm flap, produced anteriorly in a narrow, subrectangular projection; the flap is strengthened by a subtriangular thickening, and is continuous with a milky white, iridescent, resistant membrane. An extremely sticky, glutinous material lies against the flange and adheres to the mesial surface of the flap.

The thin, translucent dorsomesial wall, like that in the spermatophore of *P. schmitti*, bulges anteriorly beyond its attachment to the ventral and lateral walls along an oblique fine rib extending from the mesial lapel to the posteroproximal end of the wing (Figure 17B). The bulge, occupied by the extremity of the sperm mass enclosed in the sac, bears a triangular crest which abuts on the

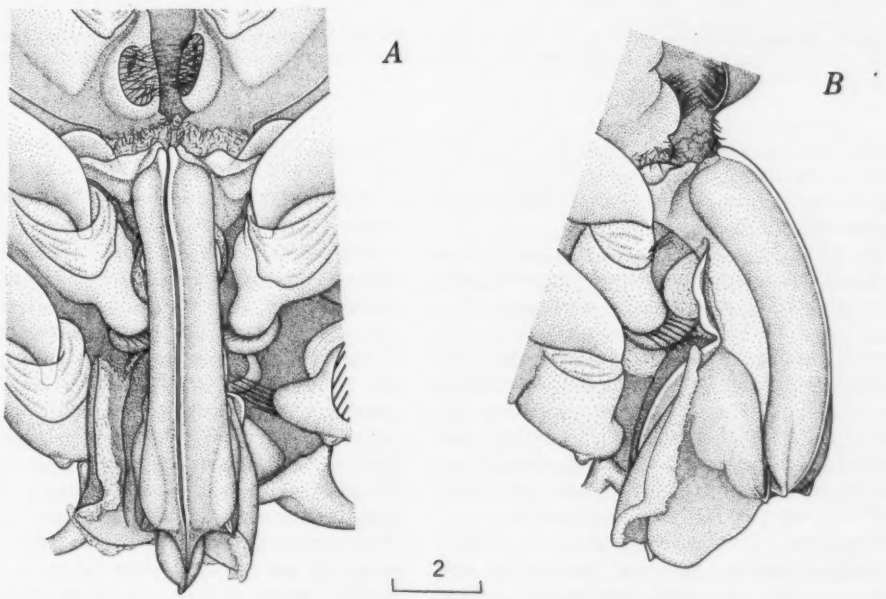

FIGURE 16.—*Penaeus* (*Litopenaeus*) *setiferus* (Linnaeus). *A*, Compound spermatophore attached to female, ♀32 mm cl, 0.8 km off Long Beach, N.C. *B*, Lateral view of same specimen.

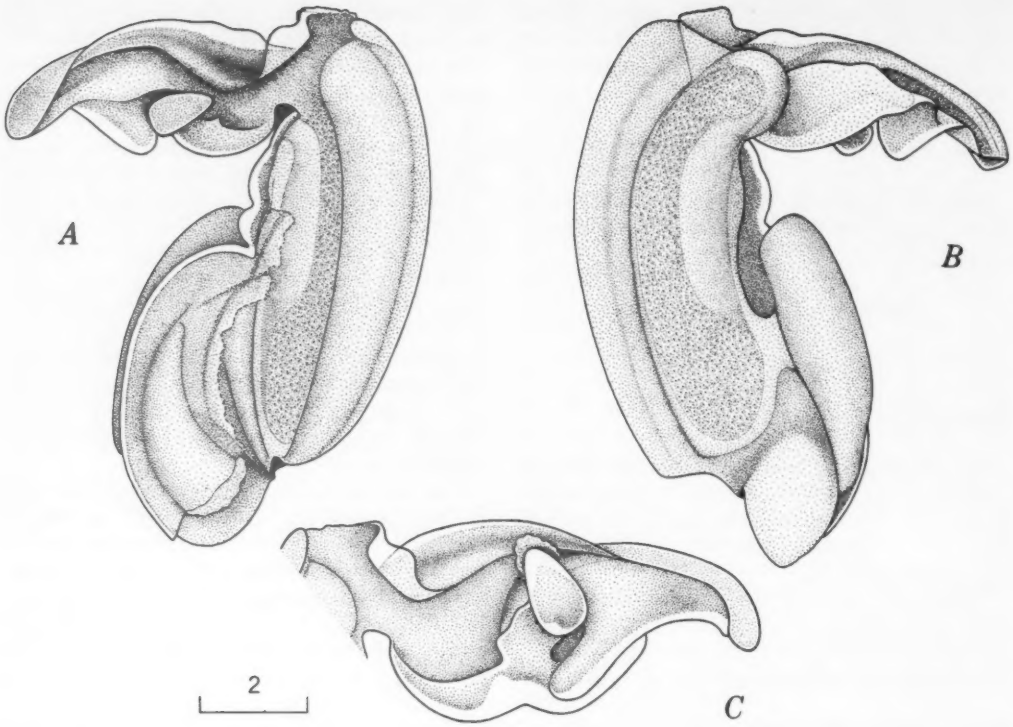

FIGURE 17.—*Penaeus* (*Litopenaeus*) *setiferus*. *A*, Ventrolateral view of right spermatophore dissected from terminal ampulla, ♂SW of mouth of Sabine River, Tex. *B*, Dorsomesial view of same specimen. *C*, Ventral view of wing, left spermatophore, ♂off Melbourne Beach, Fla.

mesial lapel; posterior to the bulge, the dorsomesial wall extends laterally to join the lateral wall (along the base of the blade), and posteriorly merges with the flange.

The wing, long and irregular in contour, is produced posteriorly in a broad proximal lobe, tapering laterally to a rounded, excavated, short tip (Figure 17C). The ventral surface is very irregular, bearing several projections: a rigid subtriangular or rounded prominence on an anterior rib; an elongate twisted process, its base continuous with a posterior fold of the proximal lobe situated about midlength, extending mesially into a subovate to semicircular flap; and a subdistal shelf obliquely flanking the twisted process.

The dorsal plate is tear-shaped in outline, rounded anteriorly, tapering posteriorly, and moderately long, extending from slightly beyond the anterior margin of the flange to its posterolateral corner.

Thelycum (Figure 18)

Sternite XIV bears a pair of sharp crescentic anterolateral ridges the posterior portions of which converge mesially but do not meet, and are often separated by a median longitudinal rib; the posterior part of this sternite is provided with a pair of closely set fleshy lobes, usually separated by a fine median rib which may be continuous with the anterior one. Sternite XIII is heavily sclerotized, forming a strong plate produced posteriorly as a soft emarginate shelf overhanging sternite XIV; the anterior part of this sternite bears a pair of soft, naked, transverse elevations flanking a tonguelike lamella bordered by setae. The lamella forms the roof of a concavity floored by a strong ridge of sternite XII. The ridge (a marginal thickening of heavily sclerotized sternite XII, mostly hidden by setose, rounded and relatively short coxal plates of the third pereopods) is almost

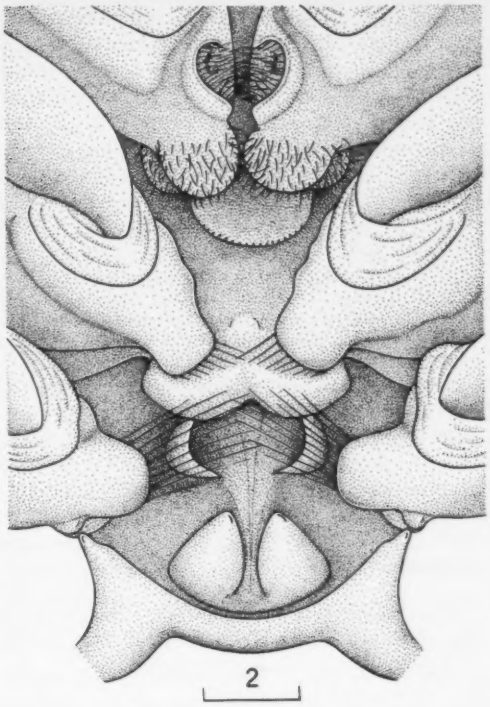

FIGURE 18.—*Penaeus* (*Litopenaeus*) *setiferus*. Thelycum, ♀40 mm cl, off Galveston, Tex.

straight or slightly emarginate along its median portion, and produced laterally in a pair of convex projections armed with long setae. The concavity of sternite XIII is most important in that it serves to lodge the sperm masses protruding anterodorsally from attached spermatophores.

Disposition of the Compound Spermatophore on the Thelycum

The compound spermatophore is anchored to the female much as it in *P. schmitti*. Anteriorly, the geminate body lies on the mesial portions of the coxal plates of the third pereopods (immediately posteroventral to the gonopores), with the sperm masses projecting anterodorsally through the ruptured bulges of the sacs, to lie in a gelatinous envelope fitting into the concavity of sternite XIII. The wings embrace the sperm masses and then extend over the coxal plates, leaving a passageway between them and the body of the animal. The wings are proximally attached to sternite XIII (just caudal to the thelycal lamella) by their posterior lobes, which are in close proximity, and distally affixed to the sternite, or partly to the latter and partly to the articular membranes of the third pereopods. Posterior to the wings, the lateral portions of the ventral walls are turned strongly mesially thus reducing somewhat the lumen of the sacs (Figure 1D). This action may be responsible in part for the transfer of the sperm masses from the sacs to the concavity of sternite XIII at the time of mating. The geminate body is elevated above the sternum so that between the wings and flanges it sometimes does not touch the animal, nor even do the accompanying paired blades, which become almost perpendicular to the sternum. Caudally, the geminate body reaches sternite XIV, where the vertical shelf formed by mesial portions of the flanges lies between the thelycal lobes, or farther beyond on the first pleonic sternite. The firm elongate flaps project ventromesially in conspicuous fashion on each side of the geminate body, whereas anterolateral portions of the flanges are horizontally applied to the dorsal plates, in turn attached to sternite XIV.

I have examined a few females carrying only those parts of the compound spermatophore which are firmly anchored to sternite XIII; the geminate body and adjoining structures have been lost. In all of them, parts remaining affixed to the thelycum (Figure 19) are almost identical: paired masses of sperm lie exposed in the concavity of sternite XIII, where each is contained in an indurate gelatinous substance which, in turn, is tightly embraced by the wings. It appears that in this species, as in *P. stylirostris*, when the spermatophores are released from the terminal ampullae of the male, the masses of sperm and jelly are transferred from the posterior parts of the sacs to the anterodorsal bulges which break under pressure allowing sperm, surrounded by jelly, to reach the thelycal concavity of sternite XIII. This gelatinous substance is directly applied to the concavity, there forming an envelope containing sperm. Eventually, the compound spermatophore splits, the geminate body falls, or is torn away, and the sperm is exposed.

In the impregnated females mentioned above, the compound spermatophore had split in the same fashion, leaving the sperm masses exposed to the surrounding water, suggesting that this rupture might be the means by which spermatozoa are

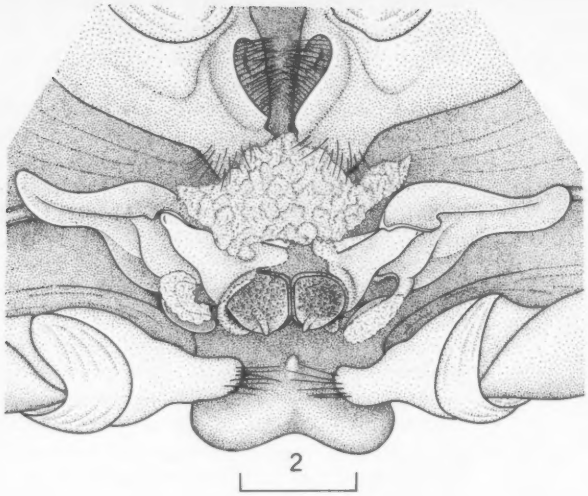

FIGURE 19.—*Penaeus* (*Litopenaeus*) *setiferus*. Sternites XII and XIII bearing wings and paired masses of sperm from a compound spermatophore the geminate body of which has been lost, ♀ 32.5 mm cl, off Long Beach, N.C.

released at the time of spawning. In some of these females, however, as well as in others with complete spermatophores, a part of each sperm mass protrudes anteriorly from the passageway between the wings and the body of the animal, and even extends onto sternite XII. This indicates that the spermatozoa might disperse anteriorly from the gelatinous envelops surrounding the paired sperm masses while the compound spermatophore is still attached to the female and otherwise intact. Thus, which of these methods is employed in the release of the sperm must await observations of live females immediately after copulation.

Material

The specimens examined by me are listed in Pérez Farfante (1969). Additional specimens follow.

UNITED STATES. 4 ♂ 3 ♀ [1♀ impregnated], UNC-IMS, 0.8 km off Long Beach, (3.2 km E of Lockwood's Folly), N.C., 6 m, 6 May 1949.- 3 ♂ 2 ♀ [impregnated], UNC-IMS, 0.8 km off Long Beach, N.C., 6 m, 6 May 1949.- 1 ♂ 2♀, [1♀ impregnated], UNC-IMS, Beaufort Bar (between Sea Buoy and Bar Buoy No. 1), N.C., 13-16 m, 6 July 1949, *Penny*.- 2♀[impregnated], USNM, Apalachicola Bay, Fla., June 1974.- 1♀ [impregnated], USNM, SE of Freeport, Tex., 15 m, 26 July 1973.- 1♀ [impregnated], USNM, off Galveston, Tex., 1973.- 20 ♂, USNM, off Galveston, Tex., 25 June 1974.

Species Range

Fire Island, N.Y., to Saint Lucie Inlet, Fla.; in the Gulf of Mexico, from west Florida to the vicinity of Ciudad Campeche, Campeche.

ROLE OF COXAL PLATES IN RETENTION OF COMPOUND SPERMATOPHORE

In the females of the various species of *Litopenaeus*, the coxal plates of the last three pairs of pereopods exhibit specific variations which seem to be associated with the position of the affixed compound spermatophore and the function they serve in holding it in place. In *P. vannamei*, in which the spermatophore reaches anteriorly only to the median protuberance of sternite XIII, the coxae of the third pereopods are not produced posteriorly into well-defined coxal plates. In contrast, the fourth pereopods bear large, flattened coxal plates offering extensive support to the anterior parts of the sperm sacs. The coxal plates of the fifth pereopods are rather short, but prominent, and directed mesially providing a base of attachment for the ventrally elevated lateral portions of the dorsal plates; thus, they are responsible in part for keeping the posterior parts of the sacs raised well above the sternum.

In *P. occidentalis*, the coxal plates of the third pereopods are very elongate and strongly curved anteromesially and dorsally in scooplike fashion,

serving to receive the sperm immediately after its release through the openings of the sperm sacs which lie immediately posteroventral to them; the enclosure for the freed sperm is completed ventrally by the bases of the anterior lobes of the spermatophores which are applied to sternite XII. The coxal plates of the fourth and fifth pereopods are relatively short but are directed mesially, helping to keep the compound spermatophore in position by supporting its lateral blades which lie dorsal to them and which are firmly applied to the thelycum.

In *P. schmitti*, *P. setiferus*, and, particularly in *P. stylirostris*, the coxal plates of the third pereopods are large and directed posteriorly; thus, they appear to aid in keeping the sperm masses (projecting dorsally through the compound spermatophore) within the thelycal concavity of sternite XIII. This is suggested by the fact that in the former two species, in which the concavity lies on the anterior part of sternite XIII, the coxal plates are much shorter than in *P. stylirostris* in which the double concavity is located on the posterior part of the sternite. In *P. schmitti* and *P. setiferus*, the coxal plates of the fourth and fifth pereopods (longer in the latter) are directed mesially, supporting the lateral components of the spermatophore and pressing them against the thelycum. In *P. stylirostris*, these coxal plates are larger than in any of the other species, those of the fifth pereopods offering a broad base for the attachment of the anterior portions of the dorsal plates of the spermatophore to their ventral surfaces. The coxal plates of the fourth pereopods are directed posteromesially, lying ventrad to the subvertical shelf of sternite XIII, thus helping in holding the sperm masses within the thelycal concavities of the latter sternite.

Finally, in all five species, the coxal plates are provided with numerous long, mesially directed setae which, in impregnated females, become embedded in the dorsal plates or extend over the blades and flanges, thus contributing to maintaining the spermatophore in position.

COMPARISONS OF SPERMATOPHORES

The morphology of the spermatophores of two species of the subgenus *Melicertus* have been studied in rather considerable detail: that of *P.* (*M.*) *kerathurus* (Forskål 1775) by Mouchet (1931) and Heldt (1938a, b), and that of *P.* (*M.*) *japonicus* Bate 1888, by Kishinouye (1900), Hudinaga (1942) and, later, more meticulously by Tirmizi (1958). A brief illustrated account of the spermatophore of *P.* (*Farfantepenaeus*)[2] *duorarum duorarum* Burkenroad 1939, was presented by Eldred (1958). Recently, Malek and Bawab (1974a, b), conducted a thorough study of the formation of the spermatophore within the vas deferens in *P.* (*M.*) *kerathurus*; the hardened cover of the spermatophore that is contributed by the ampulla is now being investigated by them. The above studies, as well as those on the subgenus *Litopenaeus*, have revealed that in spermatophores of *Penaeus* the sperm mass is surrounded by a gelatinous, multilayered (Malek and Bawab 1974b) sheath which, in turn, is enclosed in a sperm sac; this usually bears an aliform process, and in members of *Litopenaeus* additional attachment structures are present.

The principal characteristics of the spermatophores of the five species of *Litopenaeus* are presented in Table 1 to facilitate a comparison of them.

The spermatophore of *P. vannamei* is the simplest. It lacks an anterolateral wing, is not produced into an anterior lobe, and does not bear a lateral blade.The fact that the ventral and lateral walls are both opaque and thus almost indistinguishable, contributes to the relatively simple appearance of this spermatophore. However, it exhibits by far the thickest lateral flap and the largest dorsal plate. Apart from the seemingly firm affixation of the anterior part of the sacs to the thelycum, the attachment of the compound spermatophore to the female is accomplished by the very elongate dorsal plates, which support the geminate body and the paired flanges. Finally, the compound spermatophore when applied to the female extends only to about the midlength of sternite XIII, instead of reaching sternite XII as do those of the other species. The short anterior extensions of the ventral walls are applied to the median protuberance of sternite XIII, and the prominent bulges of the sacs, where the sperm masses are concentrated, lie at the anterior part of sternite XIV. Consequently, the sperm is released farther away from the gonopores of the female than in the remaining species.

[2]The subgenus *Farfantepenaeus* was recently established by Burukovskii (1972) to include the grooved species of *Penaeus* (those with adrostral sulci extending posteriorly beyond midlength of carapace) from American waters, one of them also occurring off West Africa. These shrimps were previously placed by Pérez Farfante (1969) in the subgenus *Melicertus* Rafinesque 1814, together with the grooved *Penaeus* occurring from the eastern Atlantic eastward to the waters of Hawaii.

TABLE 1.–Characteristics of the spermatophores of five species of *Penaeus (Litopenaeus)*.

Species	Sperm sac	Wing	Anterior lobe	Flange	Blade	Lateral flap		Anterior lamina	Dorsal plate	Position on female
						Along sac	Along flange			
P. vannamei	Simple[1]	Lacking	Lacking	Long, caudal	Lacking	Broad, fleshy	Narrow, flexible	Lacking	Long, underlying most of sac and flange	Reaching about mid-length of sternite XIII
P. occidentalis	Simple	Small	Present	Short, caudal	Attached at edge, extending laterally; broad	Lacking	Broad, highly sclerotized	Present	Moderately long, underlying blade	Reaching posterior part of sternite XII, and embracing gonopore
P. stylirostris	Complex[2]	Large	Lacking	Long, caudolateral	Attached along midline, extending dorsomesially and ventromesially	Broad, membranous	Narrow, flexible	Lacking	Moderately long, underlying base of sac and flange	Reaching anteriormost part of sternite XIII
P. schmitti	Simple	Moderately large	Lacking	Long, caudolateral	Attached at edge, extending laterally; broad anteriorly	Narrow, firm	Broad, firm	Lacking	Long, underlying blade and flange	Reaching anteriormost part of sternite XIII
P. setiferus	Simple	Moderately large	Lacking	Long, caudolateral	Attached at edge, extending laterally; narrow throughout	Narrow, firm	Broad, firm	Lacking	Moderately long, underlying flange	Reaching anteriormost part of sternite XIII

[1]Lateral wall continuous with dorsomesial.
[2]Lateral wall overlapping dorsomesial wall laterally, forming free shield (see p. 473).

It seems noteworthy that *P. vannamei* is the only species of the subgenus *Litopenaeus* in which a strongly developed median protuberance (projecting from sternite XIII) is present on the thelycum. Females of the remaining species of *Litopenaeus* lack a median protuberance, unlike all of the other species of *Penaeus*. In the former females, the midposterior part of sternite XIII bears instead a simple, relatively small knob–in *P. occidentalis*–or is produced into a shelf which overhangs sternite XIII. This shelf is horizontal in *P. schmitti* and *P. setiferus*, and subvertical in *P. stylirostris*.

The spermatophore of *P. occidentalis* is considerably more elaborate than that of *P. vannamei*, although the sac is structurally similar in the two and simpler than that of *P. stylirostris*. The spermatophore of *P. occidentalis*, unlike that of *P. vannamei*, possesses a wing and, unlike all other species of *Litopenaeus*, bears an anterior lobe, and is produced caudally in a very short flange. Also, it bears the largest lateral blade to be found in any of them, the blade being divided in several sections and continuous with the typical stiffened ventromesial extension, ending in a rather flexible caudal lobe; that extension seems to correspond to the flap borne by spermatophores of the other species. In addition, the spermatophore of *P. occidentalis* possesses a unique transverse lamina on the anterior extremity of the sac, which is not intimately associated or even firmly attached to it or to the other contiguous components, i.e., the anterior lobe and the wing. In this spermatophore, however, the flange is inconspicuous, consisting of a short rigid shelf at the posterior end of the sac. Finally, the compound spermatophore of *P. occidentalis* is affixed to the female farther anteriorly than in the other species, the anterior lobes extending over (ventrally) the coxae of the third pereopods to become attached to sternite XII; this brings the openings of the sacs to the scooplike coxal plates of the third pereopods, almost directly opposite the female gonopores.

The spermatophore of *P. stylirostris* differs from all the others chiefly in the structure of the sperm sac, which is largely formed by the dorsomesial wall. This wall, after extending laterally, is bent mesially in such a way as to reach, ventrally, the base of the mesial flap; as a result, part of the ventral and lateral walls, apart from giving support to the sac, serve as a protecting shield. The spermatophore of *P. stylirostris* also possesses the broadest wing to be found within the subgenus,

and is armed with a blade, the anterior portion of which is directed both dorsomesially and ventromesially instead of laterally, in specimens removed from males. Along the sac, the lateral flap is almost as broad as that in *P. vannamei*, but thinner and not fleshy. Furthermore, in *P. stylirostris*, the paired dorsal plates affix only the posterior part of the spermatophore to the females, not directly supporting the midportion. The flanges become attached to the female almost perpendicular to the geminate body, instead of extending entirely caudad as in *P. vannamei* or somewhat caudad as in *P. schmitti* and *P. setiferus*.

The spermatophores of *P. schmitti* and *P. setiferus* are almost identical. They may be distinguished by the width of the lateral blade, the anterior portion of which is broad (except for a narrow portion at the base of the wing) in *P. schmitti* and very narrow in *P. setiferus*. Sperm sacs of both species are similar to those of *P. vannamei* and *P. occidentalis*; however, they bear wings, which are lacking in *P. vannamei*, and the wings are moderately large and scabrous, with various projections on the ventral surface, thus very different from the small wing with the margins extensively folded found in *P. occidentalis*.Also, the flanges extend considerably anteriad along the lateral walls of the sacs, whereas those in *P. vannamei* are virtually caudal and, unlike *P. occidentalis*, are produced posteriorly much beyond the sac instead of barely overreaching the fundus. Finally, flaps borne by the flanges are broad in the two Atlantic species, instead of narrow as in *P. vannamei*, and, although firm, are different in texture from the heavy sclerotized shelf sustained by the flange in *P. occidentalis*.

Despite the similarities of the various sacs, the mode of dehiscence varies–differences among the spermatophores are due more to the elements associated with the sac than to the sac itself. It seems that in *P. occidentalis*, the sperm is released through anterior openings of the sacs which become applied to the coxal plates of the third pereopods, and are well protected by the anterior lobes of the spermatophores. In *P. stylirostris* as well as in *P. schmitti* and *P. setiferus*, it seems that the compound spermatophore attached to the female splits longitudinally into two parts, the geminate body breaks away leaving paired masses of sperm on the thelycum freely exposed to the surrounding water. In *P. schmitti* and *P. setiferus*, however, there are certain indications that the sperm reaches the water through a passageway between the wings and the body of the female, the geminate body persisting. On the basis of the available material of *P. vannamei*, there is no indication as to how the sperm escapes from the spermatophore. Understanding of the precise manner in which spermatozoa are freed from spermatophores in all of the species must await direct observations.

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LITERATURE CITED

BURKENROAD, M.D.

1934. The Penaeidea of Louisiana with a discussion of their world relationships. Bull. Am. Mus. Nat. Hist. 68:61-143.

1939. Further observations on Penaeidae of the northern Gulf of Mexico. Bull. Bingham Oceanogr. Collect. 6(6):1-62.

BURUKOVSKII, R. N.

1972. Some problems of the systematics and distribution of the shrimps of the genus *Penaeus*. [In Russ.] Fisheries Research in the Atlantic Ocean. Tr. Atlant. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 42:3-21. (Translated by Israel Program Sci. Transl., TT72-50101.)

CÁRDENAS FIGUEROA, M.

1952. Descripción del espermatóforo de *Penaeus stylirostris* Stimpson. Rev. Soc. Mex. Hist. Nat. 13:9-16.

ELDRED, B.

1958. Observations on the structural development of the genitalia and the impregnation of the pink shrimp, *Penaeus duorarum* Burkenroad. Fla. State Board Conserv. Mar. Lab., Tech. Ser. 23, 26 p.

EWALD, J. J.

1965. Investigaciones sobre la biología del camarón comercial en el occidente de Venezuela. Inst. Venez. Invest. Cient., Segundo Informe anual al Fondo de Investigaciones Agropecuarias. 1-128, 137-147 p.

HEEGAARD, P. E.

1953. Observations on spawning and larval history of the shrimp, *Penaeus setiferus* (L.). Publ. Inst. Mar. Sci., Univ. Tex. 3(1):73-105.

HELDT, J. H.

1938a. De l'appareil génital des Penaeidae. Relations morphologiques entre spermatophore, thelycum et petasma. Trav. Stn. Zool. Wimereux 13:349-358.

1938b. Le reproduction chez les crustacés décapodes de la famille des pénéides. Ann. Inst. Oceanogr. 18:31-206.

HUDINAGA (FUJINAGA), M.

1942. Reproduction, development and rearing of *Penaeus japonicus* Bate. Jap. J. Sci. 10:305-393.

KING, J. E.

1948. A study of the reproductive organs of the common marine shrimp, *Penaeus setiferus* (Linnaeus). Biol. Bull. (Woods Hole) 94:244-262.

KISHINOUYE, K.

1900. Japanese species of the genus *Penaeus*. J. Fish. Bur. Tokyo 8:1-29.

MALEK, S. R. A., AND F. M. BAWAB.

1974a. The formation of the spermatophore in *Penaeus kerathurus* (Forskål, 1775) (Decapoda, Penaeidae). I. The initial formation of a sperm mass. Crustaceana 26:273-285.

1974b. The formation of the spermatophore in *Penaeus kerathurus* (Forskål, 1775) (Decapoda, Penaeidae). II. The deposition of the main layers of the body and of the wing. Crustaceana 27:73-83.

MOUCHET, S.

1931. Sur l'appareil génital mâle de *Penaeus trisulcatus* Leach. Bull. Soc. Zool. Fr. 56:458-467.

PÉREZ FARFANTE, I.

1969. Western Atlantic shrimps of the genus *Penaeus*. U.S. Fish Wildl. Serv., Fish. Bull. 67:461-591.

TIRMIZI, N. M.

1958. A study of some developmental stages of the thelycum and its relation to the spermatophores in the prawn *Penaeus japonicus* Bate. Proc. Zool. Soc. Lond. 131:231-244.

WEYMOUTH, F. W., M. J. LINDNER, AND W. W. ANDERSON.

1933. Preliminary report on the life history of the common shrimp *Penaeus setiferus* (Linn.). Bull. U.S. Bur. Fish. 48:1-26.

DYNAMICS OF AMERICAN SHAD, *ALOSA SAPIDISSIMA*, RUNS IN THE DELAWARE RIVER[1]

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ABSTRACT

Adult American shad were collected by haul seining at regular intervals during the spring migrations from 1963 to 1965 and by collecting specimens from a fishkill in spring 1965. Supplementary sex and size composition data were obtained from summer rotenone sampling in 1961 and 1962.

Males tended to precede females in the spring run. Annual sex compositions were strongly male dominated from 1961 to 1963 and were strongly female dominated in 1964 and 1965. Repeat spawners composed 2.6% of 729 fish examined from 1963 to 1965. Age I and II fish were absent or virtually absent from the run. Males migrated upstream primarily at age IV and females at age V. Large runs during the early 1960's were based on the 1958 and 1959 year classes as defined which were much larger than other year classes produced in the period 1957-64. Delaware River American shad runs now have little buffering against fluctuations in abundance because few year classes are successful, few age groups support the run, and there are essentially no repeat spawners. Larger runs in the Delaware since 1925 and probably somewhat earlier, in general, were apparently based on one large year class and essentially no repeat spawners.

The American shad, *Alosa sapidissima*, formerly was one of the most abundant anadromous fishes in the United States where more than 50 million pounds were landed in 1896. In contrast, only 8 million pounds were caught in 1960 (Walburg and Nichols 1967). Much of this decline is due to the collapse of the Delaware River Basin fisheries which once supported larger landings of American shad than any other river system (Stevenson 1899). Estimates of the 1896 Delaware Basin catch are about 16.5 to 19.2 million pounds (Smith 1898; Sykes and Lehman 1957; Walburg and Nichols 1967)—about a third of the national total. Annual Delaware Basin catches about that time varied from 14 to 17 million pounds and were probably primarily fish of Delaware River origin (Chittenden 1974). In contrast, annual Delaware Basin landings since 1920 have consistently been much less than 0.5 million pounds (Sykes and Lehman 1957; Chittenden 1974).

Trends in abundance of Delaware Basin stocks have been described by Sykes and Lehman (1957) and Chittenden (1974), and causes of these fluctuations have been described by Ellis et al. (1947), Sykes and Lehman (1957), Walburg and Nichols (1967), and Chittenden (1969). The dominant factor affecting abundance during the past 60 yr, at least, has been pollution near Philadelphia, Pa. Complete understanding of the causes of fluctuations in abundance, however, depends on detailed knowledge of the population dynamics of this species. Many workers have described certain aspects of the population dynamics of American shad in other river systems. Little work has been published for the Delaware, in part because Delaware River American shad stocks have been so low that it has been difficult to collect large numbers of fish.

The present paper describes data collected on sex, size, age, and repeat spawner composition; comparative magnitudes of American shad runs; and year-class strengths in the Delaware River during the late 1950's and the 1960's.

MATERIALS AND METHODS

Adult fish were collected 22.5 km (14 miles) above tidal water in the years 1963 to 1965 at the site of the Lewis Fishery in Lambertville, N.J., using a 76-mm (3-inch) stretch-mesh, 107-m (350-foot) long and 3.6-m (12-foot) deep (4.3 m = 14 feet in 1963) haul seine that was paid out from a boat and landed about 396 m (1,300 feet) downstream. Sampling occurred at 4-day intervals after a randomly selected date in 1963 but at fixed intervals

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twice weekly in later years. Sampling occurred from 5 April to 19 May in 1963, from 20 March to 18 May in 1964 and from 26 March to 7 May in 1965. In 1964 and 1965, at least, several collections were made both before and after the first and last American shad were captured, but a few fish were captured on the first and last sampling dates in 1963. My sampling in 1963 essentially ended when the run did at Lambertville. I captured 1 fish after 15 May, and the Lewis Fishery captured 5 fish after that date of a total catch of about 4,000 fish (Chittenden 1969). The number of seine hauls and time of sampling varied each day during 1963. After 1963 two seine hauls were made from 1100 to 1300 EST on each sampling day after the first American shad was landed. In spring 1965, low dissolved oxygen levels near Philadelphia blocked upstream passage of part of the spawning run, and few fish were captured at Lambertville (Chittenden 1969). Hundreds of dead fish were collected during a fishkill seaward of Philadelphia in the area from Paulsboro, N.J., to Marcus Hook, Pa., during the period from 21 May to 10 June. Sex and size composition data for 1961 and 1962 were obtained from cooperative surveys (hereinafter referred to as the Tri-state Surveys) using rotenone during July and August by the states of New Jersey, New York, and Pennsylvania in conjunction with the U.S. Fish and Wildlife Service. I personally examined many of the American shad collected.

Each fish collected after 1962 was measured and was sexed by examination of the gonads, and scales were taken from the midline of the left side below the dorsal fin following Cating (1953) or from the same area on the right side. Many fish collected near Marcus Hook during 1965 had lost all or nearly all their scales, so scales were taken where available on these fish. Scales selected for age determination were cleaned and were dry-mounted between glass slides. Aging was done with a microprojector using Cating's (1953) method which was verified by La Pointe (1958) and Judy (1961). Scales were examined in the time sequence 1963, 1964, and 1965 for an initial determination. Many of the large fish were known to have been misaged when the sequence was completed. Scales were next thoroughly mixed to remove bias due to knowledge of the collection year and were reread. The first two readings disagreed on 31 of 301 fish (10%) from 1963, 38 of 199 (19%) from 1964, and 3 of 184 (2%) from 1965. Of these, 32 disagreements were on females reassigned from age-group V to VI (9 from 1963 and 23 from 1964). A third examination of the misaged scales agreed with the second on 67 of the 72 fish. The remaining 5 were discarded.

RESULTS AND DISCUSSION

Sex Composition of the Spawning Runs

Many American shad were captured at Lambertville during 1963 (301 fish) and 1964 (199 fish). Figure 1 shows trends in the cumulative percentage of males as these spawning runs progressed. Trends were similar during each year although the 1963 run contained a much higher percentage of males than the 1964 run. The cumulative proportion of males decreased as the run progressed in agreement with the observations or statements of many workers including Stevenson (1899), Prince (1907), Leach (1925), Hildebrand and Schroeder (1928), Nichols and Tagatz (1960), and Walburg and Nichols (1967).

Annual sex compositions of the runs from 1961 to 1965 are presented in Table 1 with 95% confidence limits for the proportion of males based upon normal approximations except for 1962 when a Poisson approximation to the binomial was used (Cochran 1953). Annual sex composition varied greatly from 1961 to 1965. It was male dominated from 1961 to 1963 and female dominated thereafter.

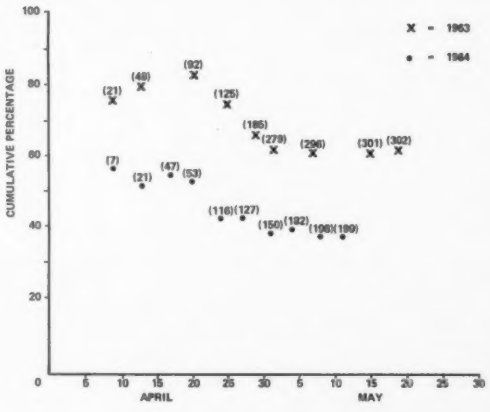

FIGURE 1.—Trends in the cumulative percentage of male American shad. Numbers in parentheses represent cumulative numbers of fish captured.

TABLE 1.–Annual sex compositions of American shad runs, 1961-65.

Year	Sample size (n)	Proportion male (p)	95% CL about p[1]
1961	198	0.86	0.81-0.94
1962	220	0.99	0.96-1.00
1963	302	0.62	0.57-0.67
1964	199	0.38	0.31-0.45
1965 Lambertville	23	0.52	0.32-0.72
1965 Tidal area	190	0.23	0.17-0.29

[1]Confidence limit for proportion of males.

Size Composition

Mean fork lengths, numbers of fish, 95% confidence limits for means, and 99% limits for individuals collected at Lambertville or the tidal area and during the Tri-state Surveys are summarized in Table 2. Data were originally expressed in total or fork length depending on year of collection. Means and confidence limits were transformed to fork lengths in inches using the regression of fork on total length presented by Chittenden (1969) and were then transformed to metric units. Females from Marcus Hook and Lambertville did not appear significantly different in size and were pooled. Males from Marcus Hook were significantly smaller ($t = 4.67$) than those from Lambertville, and they were not combined.

Fish were smaller in 1961 and 1962 than in later years, and this probably reflects the presence of very young individuals of the strong 1958 and 1959 year classes (see section "Comparative Year-Class Strengths"). Females averaged about 50 mm (2 inches) longer than males each year. Confidence limits for individuals indicate that there were few females longer than 545 mm (21.5 inches) and few males longer than 505 mm (19.9 inches). Maximum observed sizes were 559 and 495 mm (22.0 and 19.5 inches) for females and males, respectively. Small fish did not migrate upstream. The smallest female was about 64 mm (2.5 inches) longer than the smallest male each year. There were few females shorter than 416 mm (16.4 inches) in 1963, 1964, and 1965, the smallest being 406 mm (16.0 inches). The smallest female observed was 376 mm (14.8 inches) and 391 mm (15.4 inches) in 1961 and 1962, respectively. Confidence limits indicate that there were few males shorter than about 337 mm (13.2 inches) from 1962 to 1965. There were few males shorter than 289 mm (11.4 inches) in 1961, the smallest fish measured being 269 mm (10.6 inches).

Age and Repeat Spawner Comsposition

There were only 2.6% repeat spawners in 729 fish examined from 1963 to 1965. Annual occurrences were 1 of 299 fish (0.3%) in 1963, 3 of 199 (1.5%) in 1964, and 15 of 231 (6.5%) in 1965. Confidence limits for the annual percentages are 0.0 to 1.9% (1963) and 0.03 to 4.4% (1964) based upon Poisson approximations and 3.5 to 9.5% (1965) based upon the normal approximation.

Table 3 summarizes male and female age-class structures of the 1963 and 1964 runs at Lambertville, pooled data for 1965 from Lambertville and Marcus Hook, and data pooled over all years. Fluctuations in age composition due to variable year-class recruitment are apparent, but certain general features of the age composition stand out.

TABLE 2.–Summary of fork lengths of American shad, 1961-65. Lengths are in millimeters (top rows) and inches (bottom rows).

Year	Males				Females			
	n	Mean ($\bar{x}$)	95% CL $\bar{x}$[1]	99% CL x[2]	n	Mean ($\bar{x}$)	95% CL $\bar{x}$[1]	99% CL x[2]
1961	170	401	394-407	289-512	28	452	441-463	371-533
		15.8	15.5-16.0	11.4-20.1		17.8	17.4-18.2	14.6-21.0
1962	217	415	414-415	362-467	3	451	322-579	—
		16.3	16.3-16.3	14.2-18.4		17.8	12.7-22.8	—
1963	186	428	425-431	371-485	115	472	468-476	416-529
		16.9	16.7-17.0	14.6-19.1		18.6	18.4-18.8	16.4-20.8
1964	76	427	420-434	350-504	122	480	477-484	428-533
		16.8	16.6-17.1	13.8-19.8		18.9	18.8-19.1	16.9-21.0
1965	12	436	417-455	342-530	11	483	472-495	431-536
Lambertville		17.2	16.4-17.9	13.5-20.9		19.0	18.6-19.5	17.0-21.1
1965	43	417	408-426	337-498	147	484	480-488	422-546
Tidal area		16.4	16.1-16.8	13.2-19.6		19.1	18.9-19.2	16.6-21.5
1965	—	—	—	—	158	484	481-488	423-545
Combined		—	—	—		19.1	18.9-19.2	16.7-21.5

[1]Confidence limit for mean fork length.
[2]Confidence limit for indivdual fish collected.

TABLE 3.—Age-class structures of American shad, 1963-65.

Age	1963		1964		1965		Total	
	n	%	*n*	%	*n*	%	*n*	%
				Males				
II	0	0	1	1	0	0	1	0.00
III	4	2	1	1	3	6	8	2.58
IV	149	82	51	68	36	68	236	76.13
V	27	15	21	28	14	26	62	20.00
VI	2	1	1	1	0	0	3	0.01
				Females				
IV	31	27	9	7	10	8	50	13.70
V	63	56	77	64	85	65	225	61.64
VI	19	17	35	29	34	26	88	24.11
VII	0	0	0	0	2	2	2	0.01

The following comments essentially apply to virgin fish because the percentage of repeat spawners was negligible.

Age I and II males did not migrate upstream, although one age II male was captured in 1964. Few age III males migrated upstream, the percentage based on pooled data over all years being less than 3%. Males migrated upstream primarily at age IV (76%), but age V (20%) was also important. Few males survived to age VI, and all were virgin. No males older than age VI were captured. No females younger than age IV or older than age VII were observed. Only two age VII females (less than 1% of the pooled total) were captured, and one of these was a virgin. Females were primarily age V (62%) when they first entered the fishery, but ages IV (14%) and VI (24%) were also important.

Comparative Magnitudes of American Shad Runs, 1961-68

I here define magnitude of American shad runs as the numbers of adults reaching Lambertville on their upstream migration. The magnitude of runs as defined is influenced by year-class strength as later defined herein and by dissolved oxygen levels that the adults encounter during migration upstream past the Philadelphia area (Chittenden 1969). Chittenden examined in detail the annual effects of oxygen upon passage of adults and young. In general, dissolved oxygen is sufficiently high that the earlier stages, at least, of the adult run successfully migrate upstream.

Reasonably precise estimates of the comparative magnitudes of American shad runs in the 1960's are available from three sources of evidence: 1) catches of the Lewis Fishery at Lambertville presented by Chittenden (1974), 2) my own catches at Lambertville, and 3) sex compositions of the runs presented in Table 1.

Lewis Fishery annual catch/seine haul records indicate the comparative magnitudes of runs in descending size order were: 1963 (56.1 fish), 1964 (18.3), 1962 (13.9), 1965 (6.6), 1967 (3.7) = 1961 (3.5), and 1966 (1.8) = 1968 (1.2). Values in parentheses represent catch/seine haul. My annual catch/seine haul at Lambertville for the time period between capture of the first and last fish was 17.4 fish in 1963, 9.0 in 1964, and 3.0 in 1965, a pattern in agreement with the Lewis Fishery records. My general impressions derived from angling experience, interviews with other anglers, and visual observations of the abundance of adult American shad during extensive float trips each year from 1961 to 1974 are in general agreement with the patterns suggested by the Lewis Fishery records. Runs were much smaller from 1966 to 1968 than from 1962 to 1964. The size of the run in 1965 (and possibly 1961 based on my general impressions) was intermediate between the sizes in these two periods.

The relative magnitudes of runs estimated from sex composition data (Table 1) agree with patterns indicated by catch records at Lambertville. The sex ratio shift from 1963 to 1964 suggests passage through the fishery of a year class stronger than the one immediately following because males tend to enter the run a year earlier than females. This indicates the 1963 run was larger than that in 1964.

The male proportion at Lambertville in 1965 (0.52) is biased towards the high side because the later part of the run was blocked by low dissolved oxygen near Philadelphia. The male run was much greater in 1963 than in 1964. Confidence limits for the male proportion of fish collected at Marcus Hook in 1965 were much lower than any single daily male proportion in 1963 (Figure 1) but were similar to the lowest daily male proportion in 1964. Therefore, the 1965 run was probably similar in sex composition to that of 1964. Females enter the run a year older than males. Unless females suffer a much lower annual mortality, similarity of sex compositions suggests that the 1965 run was smaller than the 1964 run—even before the fish reached the Philadelphia area. The high female proportion in 1965 suggests an even smaller run was due in 1966, another year when low oxygen levels blocked part of the run (Chittenden 1969). Dissolved oxygen was sufficiently high throughout the 1967 run to permit large numbers of fish to reach Lambertville (Chittenden 1969). The Lewis Fishery in 1967 did not make large catches to reflect 1968 males or females associated with the

1966 males, suggesting that the 1966 and 1968 runs were small–even before the fish reached the Philadelphia area.

The higher proportion of males in 1962 than in 1961 indicates that the 1962 run was larger than the 1961 run.

Comparative Year-Class Strengths, 1956-64

I here define year-class strength as the numbers of young which exist at some constant point in time–say 1 January–after the entire year class has "passed" seaward through the grossly polluted Philadelphia area. Year-class strength is influenced by spawning success. However, the dominant factor, by far, in setting year-class strength in the Delaware River is the success with which the young pass seaward through the Philadelphia area in summer and fall (Chittenden 1969).

Comparative year-class strengths can be estimated from the age and sex compositions from 1963 to 1965 (Tables 1, 3) supported by estimates of comparative run sizes. Males usually first migrate upstream at age IV and females at age V, so that the size of a run chiefly reflects the strength of year classes produced 4 and 5 yr earlier assuming constant survival at sea. Therefore, American shad runs from 1961 to 1968 chiefly reflect year-class strengths from 1956 to 1964. The largest year classes as defined were produced from 1957 to 1960 because the largest runs were from 1962 to 1964.

The 1963 American shad run was the largest in this period and primarily reflects the 1958 and 1959 year classes. I captured 90 age V fish at Lambertville in 1963 and 98 in 1964 with approximately equal effort, suggesting that the 1958 and 1959 year classes were similar. This agrees with comparative magnitude estimates for the 1962 and 1963 runs. The 1963 run was based on two large year classes and was larger than the 1962 run which was based on one large and one smaller year class.

The 1960 and 1959 year classes can be compared. I collected 180 age IV fish at Lambertville in 1963 but only 60 age IV's in 1964. This suggests that the 1959 and, by inference, 1958 year classes were much larger than that of 1960. This deduction is supported by the shift in sex composition from 1963 to 1964, which indicates the age V year class from 1959 was much stronger than the age IV year class from 1960. The 1963 run was based on two large year classes and was larger than the 1964 run which was based on one large and one smaller year class.

The 1957 and 1958 year classes can be compared. At Lambertville, 36 and 21 age VI fish were captured in 1964 and 1963, respectively, suggesting that the 1958 and, by inference, 1959 year classes were stronger than that of 1957. This is supported by mean sizes of males collected during the Tri-state Surveys of 1961 and 1962 (Table 2). The 1961 fish (mean = 401 mm = 15.8 inches) were significantly smaller than the 1962 fish (mean = 414 mm = 16.3 inches). The observed mean fork length of age IV males in 1963 and 1964 was about 422 mm (16.6 inches) (Chittenden 1969, table 17), suggesting that age III fish from 1958 were important in the 1961 run.

The 1961 and 1960 year classes can be compared. Sex composition and catch data show that the 1964 run was smaller than the 1965 run. Age structures were almost identical, however, and this indicates that the 1961 year class was smaller than that of 1960.

The strength of the 1962, 1963, and 1964 year classes as defined must have been small, probably being no larger than the 1961 year class, because the 1966 to 1968 runs were very small.

In summary, the 1958 and 1959 year classes were extremely large in comparison to the year classes produced in the period 1961-64. The 1957 and 1960 year classes were much smaller than those of 1958 and 1959, but were larger than the 1962, 1963, and 1964 year classes.

GENERAL DISCUSSION

Delaware River American shad runs in the 1960's showed great shifts in the proportion of male fish. This variation was due, in large part, to fluctuations in year-class strength. The proportions in 1961 (0.86) and 1962 (0.99) are extreme. They are based upon summer collections and are biased if females tend to return seaward earlier than males do. However, these proportions also probably primarily reflect the temporary resurgence of the Delaware River American shad runs in the early 1960's reported by Chittenden (1974). The magnitude of American shad runs in the Delaware River was at a very low level prior to 1961, increased in 1961 and 1962, and in 1963 the magnitude was such that it ranked among the largest runs in the last 45 yr or more. Because Delaware River males tend to undertake their first

spawning migration at age IV and females at age V, the strongly male dominated runs of 1961 and 1962 reflect the entry of unusually large year classes into the fishery. The magnitude of the spawning runs declined greatly after 1963, and the shift towards female dominance reflects the failure of new year classes to be recruited. The strength of the 1962, 1963, and 1964 year classes as defined was small because the 1966 to 1968 runs were very small. Yet, from visual observations and collections of young during the summer, Chittenden (1969) concluded that strong year classes were produced throughout the period 1962-66. I presented dissolved oxygen data for the periods when the young passed the Philadelphia area each year and ascribed the failure of these strong year classes to later recruit to the fishery to catastrophic destruction of the young as they passed through the grossly polluted area.

There was a negligible percentage of repeat spawners in the Delaware River American shad runs from 1963 to 1965, and there were no repeat spawners among 245 American shad collected from the 1961 run (J. Malcolm, pers. commun.). The existence of numerically few repeat spawners must have continued to be the case after 1965 because the runs from 1966 to 1968 were very small. Delaware River runs apparently have included few repeat spawners for at least some 25 yr because Sykes and Lehman (1957) reported that less than 2% of 423 fish captured in 1944, 1945, 1947, and 1952 were repeat spawners. Even the production of very large year classes appears to have little effect on the percentage of repeat spawners in the Delaware River. The percentage was only 6.5% in 1965, a year when the very strong 1958 and 1959 year classes should have increased the percentage greatly rather than by only a few points. As Sykes and Lehman (1957) pointed out, the virtual absence of repeat spawners in the Delaware River is very unlike that in other middle-North Atlantic coast rivers where repeat spawner percentages have been: St. Johns River, N.B., Canada, 22-81% (Leggett 1969); Connecticut River, 14-60% (Moss 1946; Nichols and Tagatz 1960; Leggett 1969); Hudson River, 51% (Talbot 1954); Susquehanna River, 37% (La Pointe 1958); Potomac River, 17% (Walburg and Sykes 1957); York River, 21-27% (Nichols and Massmann 1963; Leggett 1969); James River, 27%, (Walburg and Sykes 1957). Some of the higher percentages of repeat spawners in these rivers are undoubtedly biased towards the high side because they are based on collections of fish from hightly selective commercial gill nets. However, it appears that the Delaware River has a much lower percentage of repeat spawners. The Delaware River seems most like rivers south of Cape Hatteras, N.C., where few repeat spawners have been reported: Neuse River, less than 3% (La Pointe 1958; Walburg 1957); Edisto River, 0% (Walburg 1956); Ogeechee River, 0% (Sykes 1956); Altamaha River, 0% (Godwin and McBay 1967; Godwin 1968); St. Jones River, Fla., 0% (Walburg 1960; Leggett 1969).

Age-class structures of American shad runs have been reported by many workers including Talbot (1954), Fredin (1954), Walburg (1956, 1957, 1960, 1961), Walburg and Sykes (1957), Sykes (1956), La Pointe (1958), Nichols and Tagatz (1960), Nichols and Massmann (1963), Godwin (1968), and Leggett (1969). Walburg and Nichols (1967) summarized the available information by stating that age IV and V fish make up the bulk of the catch in South Atlantic rivers and Chesapeake Bay tributaries while the catch is primarily composed of age IV to VII fish in middle Atlantic rivers. Delaware River runs in the 1960's were primarily supported by age IV and V fish, although age VI females were also important. Sykes and Lehman (1957) reported similar findings for fish collected in the 1940's and 1952 except that they gave more weight to age VI fish, possibly due to sampling with commercial gill nets.

Because of the absence of repeat spawners, which tend to be older fish, few age-groups support American shad runs in the Delaware River. This is similar to the situation in South Atlantic rivers but unlike that in North Atlantic rivers. The apparent similarity of Delaware River American shad to those of southern rivers rather than to geographically more closely related fish from northern rivers is an artifact caused by man. Howell (1837) reported that American shad captured in the Delaware River averaged about 3,175 g (7.00 pounds). In contrast, Chittenden (1969) reported that males averaged 1,107 g (2.44 pounds) with 95% confidence limits about the mean being 1,080-1,134 g (2.38-2.50 pounds) and females averaged 1,737 g (3.83 pounds) with the 95% confidence limits being 1,701-1,774 g (3.75-3.91 pounds). The older age-classes obviously present in Howell's time are now absent, primarily due to pollution and fishing activities. Sykes and Lehman (1957) and Chittenden (1969) attributed the virtual absence of repeat spawners to mortality of adults in low oxygen water near Philadelphia as they

migrate seaward after spawning. Added to this is a large postspawning mortality in nontidal water (Chittenden 1969). Fishing, in general, decreases the age of the stock exploited. The historical and recent effect of fishing on Delaware River stocks is not completely clear, but this was probably a much more important factor before 1910 when commercial landings were as high as 14 to 17 million pounds annually (Sykes and Lehman 1957; Chittenden 1974). White et al. (1969) tagging studies suggested that in recent years the fishing rate was probably 20%.

The larger runs in the Delaware River in the early 1960's appear to have been primarily based upon one large year class except in 1963, when two large year classes were involved. Because few age-classes and only one year class support the run each year, Delaware River American shad stocks have little buffering against fluctuations in abundance due to adverse natural or man-made environmental factors. Large fluctuations, in fact, do appear in the catch records of the Lewis Fishery since 1925 (Chittenden 1974, fig. 3). The Lewis Fishery records show large runs over a 1- or 2-yr period intermixed with stable periods when the run was of small magnitude. This is the pattern which would be expected when the fishery is supported by one year class in which males tend to enter the fishery a year before the females and there are essentially no repeat spawners. Therefore, it appears probable that sine 1925, at least, larger runs in the Delaware River have been based upon one large year class and essentially no repeat spawners.

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LITERATURE CITED

CATING, J. P.
1953. Determining age of Atlantic shad from their scales. U.S. Fish Wildl. Serv., Fish. Bull. 54:187-199.

CHITTENDEN, M. E., JR.
1969. Life history and ecology of the American shad, Alosa sapidissima, in the Delaware River. Ph.D. Thesis, Rutgers Univ., New Brunswick, N.J., 458 p.
1974. Trends in the abundance of American shad, *Alosa sapidissima*, in the Delaware River Basin. Chesapeake Sci. 15:96-103.

COCHRAN, W. G.
1953. Sampling techniques. John Wiley & Sons, Inc., N.Y., 330 p.

ELLIS, M. M., B. A. WESTFALL, D. K. MEYER, AND W. S. PLATNER.
1947. Water quality studies of the Delaware River with reference to shad migration. U.S. Fish Wildl. Serv., Spec. Sci. Rep. 38, 19 p.

FREDIN, R. A.
1954. Causes of fluctuations in abundance of Connecticut River shad. U.S. Fish Wildl. Serv., Fish. Bull. 54:247-259.

GODWIN, W. F.
1968. The shad fishery of the Altamaha River, Georgia. Ga. Game Fish Comm., Mar. Fish. Div., Contrib. Ser. 8, 39 p.

GODWIN, W. F., AND L. G. MCBAY.
1967. Preliminary studies of the shad fishery of the Altamaha River, Georgia. Ga. Game Fish Comm., Mar. Fish. Div., Contrib. Ser. 2, 24 p.

HILDEBRAND, S. F., AND W. C. SCHROEDER.
1928. Fishes of Chesapeake Bay. U.S. Bur. Fish., Bull. 43(1):1-366.

HOWELL, S.
1837. Notice of the shad and shad fisheries of the river Delaware. Am. J. Sci. Arts 32:134-140.

JUDY, M. H.
1961. Validity of age determination from scales of marked American shad. U.S. Fish Wildl. Serv., Fish. Bull. 61:161-170.

LA POINTE, D. F.
1958. Age and growth of the American shad, from three Atlantic coast rivers. Trans. Am. Fish. Soc. 87:139-150.

LEACH, G. C.
1925. Artificial progagation of shad. Rep. U.S. Comm. Fish. 1924. Append. 8:459-486. (Doc. 981.)

LEGGETT, W. C.
1969. A study of the reproductive potential of the American shad (Alosa sapidissima) in the Connecticut River, and of the possible effects of natural or man induced changes in

the population structure of the species on its reproductive success. Conn. Res. Comm., Essex Mar. Lab., Essex, Conn., 72 p.

MOSS, D. D.
1946. Preliminary studies of the shad (*Alosa sapidissima*) catch in the lower Connecticut River, 1944. North Am. Wildl. Conf. Trans. 11:230-239.

NICHOLS, P. R., AND W. H. MASSMANN.
1963. Abundance, age, and fecundity of shad, York River, Va., 1953-59. U.S. Fish Wildl. Serv., Fish. Bull. 63:179-187.

NICHOLS, P. R., AND M. E. TAGATZ.
1960. Creel census Connecticut River shad sport fishery, 1957-58, and estimate of catch, 1941-56. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 351, 12 p.

PRINCE, E. E.
1907. The eggs and early life-history of the herring, gaspereau, shad and other clupeoids. Contrib. Can. Biol. 1902-1905:95-110.

SMITH, H. M.
1898. Report of the division of statistics and methods of the fisheries. U.S. Comm. Fish Fish., Part 23, Rep. Comm. 1897:CXXIV-CXLVI.

STEVENSON, C. H.
1899. The shad fisheries of the Atlantic coast of the United States. U.S. Comm. Fish Fish., Part 24, Rep. Comm. 1898:101-269.

SYKES, J. E.
1956. Shad fishery of the Ogeechee River, Georgia, in 1954. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 191, 11 p.

SYKES, J. E., AND B. A. LEHMAN.
1957. Past and present Delaware River shad fishery and considerations for its future. U.S. Fish Wildl. Serv., Res. Rep. 46, 25 p.

TALBOT, G. B.
1954. Factors associated with fluctuations in abundance of Hudson River shad. U.S. Fish Wildl. Serv., Fish. Bull. 56:373-413.

WALBURG, C. H.
1956. Commercial and sport shad fisheries of the Edisto River South Carolina, 1955. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 187, 9 p.
1957. Neuse River shad investigations, 1953. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 206, 13 p.
1960. Abundance and life history of shad, St. Johns River, Florida. U.S. Fish Wildl. Serv., Fish. Bull. 60:487-501.
1961. Natural mortality of American shad. Trans. Am. Fish. Soc. 90:228-230.

WALBURG, C. H., AND P. R. NICHOLS.
1967. Biology and management of the American shad and status of the fisheries, Atlantic Coast of the United States, 1960. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 550, 105 p.

WALBURG, C. H., AND J. E. SYKES.
1957. Shad fishery of Chesapeake Bay with special emphasis on the fishery of Virginia. U.S. Fish. Wildl. Serv., Res. Rep. 48, 26 p.

WHITE, R. L., J. T. LANE, AND P. E. HAMER.
1969. Population and migration study of major anadromous fish. N.J. Dep. Conserv. Econ. Dev., Div. Fish Game, Bur. Fish., Misc. Rep. 3M, 6 p.

SELECTIVE AND UNSELECTIVE EXPLOITATION OF EXPERIMENTAL POPULATIONS OF *TILAPIA MOSSAMBICA*

RALPH P. SILLIMAN[1]

ABSTRACT

Two populations of *Tilapia mossambica* were grown under controlled conditions. After a period of growth and stabilization at about 10 kg and 200 fish, exploitation was started; about 50 fish of outside stock were added to each population to increase genetic variability.

Initial exploitation at 10% (later 20%) per 2 mo encompassed all sizes above fry in the unselectively fished population. In the selectively fished population, exploitation was practiced only on fish that could not pass through 25-mm (later 22-mm) vertical slots between glass bars.

Recruitment was estimated from data of stock, mortality, and catch. Parabolas fitted to the stock-recruitment relation suggested greater recruitment in the selectively fished stock than in the unselectively fished one.

Rectilinear thickness-length regressions were calculated for immature and male fish and separately for females.

The exploitation-yield relation was assessed by fitting Fox surplus-yield models to both populations. These revealed a greater maximum sustainable yield in weight from the unselectively fished population than from the selectively fished one. Efficiency of food conversion was 29-36%.

To test for genetic effect of selection, a group of 46 fish, matched as closely as possible in size and sex composition, was selected from each population. Growth in length over a period of 150 days was significantly greater among males from the unselectively fished population than among those from the selectively fished one. Growth in length of females was practically identical for both groups. Growth in total weight was distinctly greater for the group from the unselectively fished population than from the selectively fished one.

As applied to commercial fisheries, the experimental results suggested fishing as wide a range of sizes as possible. If economic gains from selection are indicated, they should be balanced against possible costs in reduced yield and retarded growth rate.

Controlled selective breeding for desirable attributes in plants and animals is a well-recognized technique in agriculture. This technique has also had limited application in fish culture, particularly with trout. Claimed achievements have included increased size and earlier age at maturity. Fishery biologists have speculated whether the reverse process, attainment of undesirable attributes, may have occurred in some fished populations because of inadvertent imposition of selection by the fishery. Although gill nets and trawls are perhaps the most obvious gear elements causing selection, the phenomenon is probably present to some extent with practically all fishing gears. It thus becomes a matter of considerable economic importance to determine if gear selectivity has adversely affected fish stocks.

The general subject of selection for slow growth by fishing was briefly reviewed by Miller (1957). He adduced no data, however, and drew no firm conclusions, merely noting that he knew of no instances where changed growth rates in fish could not be attributed to some cause other than genetic change. It seems entirely possible, nevertheless, that such a change could occur, if selection were of sufficient strength and continued during a sufficient number of generations. Such a possibility is indicated by the success of artificial selection in altering quantitative characters in a wide variety of organisms.

The purpose of the work reported herein was to test experimentally whether selective fishing could produce a genetic change in the growth pattern of the fish in the fished stock. This problem was approached by growing two populations of Mozambique tilapia, *Tilapia mossambica*, under as nearly identical conditions as possible. One of these was then fished selectively from only those fish above a fixed thickness. The other was fished over the entire range of sizes, except the small "fry."

A secondary purpose was to compare amount and size composition of the yields under selective

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and unselective fishing. To achieve this comparison, records of weight and size composition were kept for each catch made during the experiments.

MATERIALS AND METHODS

For the experimental animal, *Tilapia mossambica* was chosen. This species is hardy and will grow readily in experimental tanks. It also is used widely in tropical pond culture and thus has some economic importance. Since it is a mouth breeder, handling and exploitation were done only at approximately 2-mo intervals.

Tanks, feeding, etc. were as reported in Silliman (1970) and represented a modification of the methods of Uchida and King (1962). Briefly summarized, the procedures were to raise the two populations in hatchery-type troughs of 850-liter (225-gallon) capacity. Water condition was maintained either by changing it biweekly or by a continuous dribbling flow into the head of each trough plus bimonthly partial changing. Temperature was maintained at 80° ± 5°F or 26.7°C (weekly means). Illumination was by fluorescent light 12 h per day. Feeding schedules and water condition are detailed in Tables 1 and 2.

Rectangular enclosures at the standpipe ends were separated from the rest of the troughs by plates with 3-mm holes through which the newly expectorated "fry" could escape, thus furnishing them refuges from cannibalism by the adults. After each counting, all fish in the refuges were placed in the main part of the tanks.

Fishing was done at approximately 2-mo intervals by removing each nth fish for fishing rate $1/n$ (n was always an integer). For the selectively fished population, all fish were placed on one side of a grid consisting of 25-mm diameter vertical glass rods spaced 25 mm (22 mm in latter part of experiment) apart. All fish were provided an opportunity to swim through the spaces between the rods; only those which could not do so were fished. In the unselectively fished population all sizes were fished except the fry (under 4-mm thickness).

Counting was done simply by netting fish from one container to another. For weighing, fish were drained in a net and then placed in a previously weighed container of water. Fish weight was obtained by subtracting the tare from the total.

All caught fish and the preexploitation stocks were measured for thickness and length. They were categorized as immature (where sex could not be determined by external inspection), male, and female. Sex determination was based on the characteristics set forth by St. Amant (1966). Length (total length to outermost tip of caudal fin) was measured on a board with millimeter scale and head block. Thickness was measured on the same device, plus a sliding block; the fish were held upright between the sliding block and the head block with firm pressure for the thickness measurement. Fish for the pretest measurements

TABLE 1.—Food placed in tanks, grams.

Date[1]	Month	Day of week	Trout pellets		Tropical fish food		Total
			Moist	Dry	A[2]	B[2]	
15 Aug. 1966	0.5-40.2	Sun.	30	10	4	5	49
to		Mon.	40	10	4	10	64
6 Dec. 1969		Tues.	40	10	4	10	64
		Wed.	40	10	4	10	64
		Thurs.	40	10	4	10	64
		Fri.	40	10	4	10	64
		Sat.	40	10	4	10	64
		Total	270	70	28	65	433
7 Dec. 1969	40.2-82.2	Sun.	30	10	4	5	49
to		Mon.	40	10	4	10	64
5 June 1973		Tues.	40	10	4	10	64
		Wed.	40	10	4	10	64
		Thurs.	40	10	4	10	64
		Fri. A.M.	40	10	4	10	64
		Fri. P.M.[3]	40	10	4	10	64
		Total	270	70	28	65	433

[1]Diet was varied initially to achieve optimal reproduction and growth; it was stabilized at the listed amounts on 18 June 1967, month 10.6.
[2]Commercal makes of dry food.
[3]This feeding was combined with the Friday A.M. feeding in 37 out of 183 wk. and with the Sunday feeding once.

TABLE 2.—Water condition on selected dates.[1]

Date	Month	O_2 (ppm.) Test[2]	O_2 (ppm.) Control[3]	CO_2 (ppm.) Test[2]	CO_2 (ppm.) Control[3]	pH Test[2]	pH Control[3]
1968:							
9	Aug.	24.3	5.2	5.0	—	—	—	—
16		24.5	4.6	4.4	—	—	—	—
29		24.9	4.8	4.8	10	10	6.9	6.9
6	Sept.	25.2	3.6	3.8	—	—	—	—
13		25.4	3.6	3.6	—	—	—	—
20		25.7	4.0	4.4	10	10	—	—
27		25.9	4.0	4.0	—	—	—	—
4	Oct.	26.1	4.0	4.4	—	—	—	—
11		26.4	3.8	4.0	—	—	—	—
18		26.6	3.0	3.8	—	—	—	—
25		26.8	3.0	4.0	—	—	—	—
8	Nov.	27.3	3.6	4.0	—	—	—	—
15		27.5	3.4	4.0	—	—	—	—
28		27.9	4.2	4.4	—	—	—	—
6	Dec.	28.2	3.8	4.0	—	—	—	—
13		28.4	3.4	4.0	—	—	—	—
26		28.8	3.0	3.4	—	—	—	—
1969:							
2	Jan.	29.1	3.4	3.6	—	—	—	—
17	Sept.	37.6	5.2	4.8	10	10	6.5	6.7
2	Oct.	38.1	5.4	5.4	—	—	—	—
9		38.3	5.0	4.8	—	—	—	—
23		38.7	5.0	4.8	—	—	—	—
30		39.0	5.4	5.0	—	—	—	—
1971:							
25-26	Feb.	54.9	4.6	4.4	20	20	6.0	6.0
1972:							
23	Mar.	67.7	3.4	[4]2.6	20	25	6.5	6.5
1973:							
29	May	81.9	3.4	3.2	15	15	7.0	7.0

[1]With the exception noted in footnote 4, all values were within (or above for oxygen) the ranges stated to be suitable for warm-water fishes by Lewis (1963). These were: oxygen, 3-5 ppm.; carbon dioxide, below 30 ppm.; pH, 5-9.
[2]Selectively fished.
[3]Unselectively fished.
[4]Aeration was increased and O_2 had risen to 3.8 ppm. by the next day.

were anesthetized with MS-222 [2] (tricaine methanesulfonate) in a 1:2,500 solution. Caught fish were measured some time after removal. They were usually alive or freshly dead, and rigor mortis was rare. The group selected for growth study at the end of the experiment was measured alive without an anesthetic.

COURSE OF POPULATIONS

A single population was started on 15 August 1966, but this was divided into two populations as nearly equal as possible after 2 mo. A period of population growth then ensued (Table 3, Figures 1, 2). This growth was extensively discussed by Silliman (1970), who found growth in biomass of the two populations to be practically identical. He therefore combined the two populations for growth analysis. A Gompertz curve fitted to the total biomass of both populations had the formula $W_t = 1.337 \exp[2.85 - 2.85 \exp(-0.2\,(t-3.6))]$, where W_t is biomass in kilograms at the time t in months. The asymptote of this curve was 23.1 kg or 11.55 kg per population. An accidental interruption to population growth (Figures 1, 2) resulted from temporary relocation of the fish during refinishing of the laboratory floor. After recovery and re-equalization, the populations did not approach the asymptote predicted by the Gompertz curve but leveled off at about 10 kg each.

Because the fish were descendants of an original three males and three females, I felt that in-

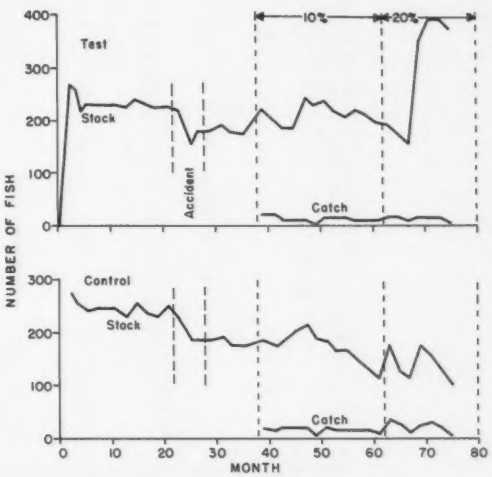

FIGURE 1.—Population size and catch, numbers. Percentages indicate target exploitation rates. Test population was selectively fished; control, unselectively.

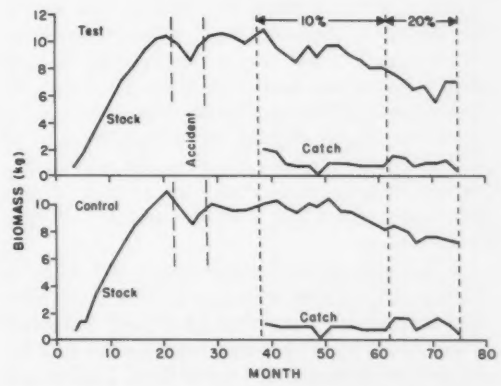

FIGURE 2.—Population size and catch, weight. Percentages indicate target exploitation rates. Test population was selectively fished; control, unselectively.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 3.–Population and catch, *Tilapia mossambica*.

Month[1]	Target expl. rate[2]	Test (selectively fished) population				Control (unselectively fished) population			
		Number		Weight (g)		Number		Weight (g)	
		Stock	Catch	Stock	Catch	Stock	Catch	Stock	Catch
0.5	0.00	6	—	—	—	—	—	—	—
2.5		272	—	—	—	273	—	—	—
3.6		258	—	856	—	253	—	825	—
4.5		220	—	1,318	—	251	—	1,325	—
5.5		231	—	1,924	—	239	—	1,447	—
7.5		228	—	3,306	—	247	—	3,303	—
10.5		228	—	5,614	—	246	—	5,749	—
13.0		224	—	7,420	—	232	—	7,313	—
15.0		239	—	8,275	—	253	—	8,692	—
17.1		228	—	9,346	—	237	—	9,448	—
19.2		226	—	10,174	—	232	—	10,244	—
21.1		224	—	10,459	—	251	—	10,907	—
23.2		[3]221	—	[3]9,859	—	[3]226	—	[3]9,826	—
25.4		[3]156	—	[3]8,567	—	[3]186	—	[3]8,561	—
27.2		181	—	9,560	—	184	—	9,431	—
29.1		180	—	10,415	—	183	—	9,967	—
31.3		189	—	10,525	—	189	—	9,791	—
33.1		181	—	10,348	—	177	—	9,622	—
35.3		177	—	9,881	—	173	—	9,661	—
39.2	0.10	218	19	10,760	2,023	183	18	10,009	1,168
41.3		201	18	9,468	1,714	174	17	10,139	1,033
43.2		187	8	8,984	906	187	18	9,743	974
45.2		187	8	8,311	794	199	19	9,300	956
47.3		[4]240	8	[4]9,534	883	[4]217	22	[4]9,917	909
48.9		231	2	8,860	182	191	4	9,843	191
51.2		233	14	9,690	960	186	18	10,368	1,057
53.2		217	14	9,575	991	163	16	9,532	927
55.1		207	14	9,037	929	165	16	9,315	951
57.2		221	12	8,542	848	148	15	8,956	895
59.0		210	10	8,056	806	131	13	8,507	827
61.1		196	10	7,935	853	117	12	8,287	824
63.2	0.20	191	17	7,687	1,575	177	35	8,322	1,681
65.4		172	17	6,944	1,377	124	25	7,965	1,531
67.1		157	11	6,382	738	114	12	7,261	840
69.1		345	15	6,684	1,050	176	26	7,592	1,217
71.2		388	14	5,465	1,061	155	31	7,664	1,574
73.2		389	14	7,046	1,170	123	21	7,389	1,272
75.1		371	6	6,901	438	101	6	7,280	459

[1]0 = 1 August 1966.
[2]Because of selection problems, actual rates varied considerably from these. In analyses, effective rates in terms of weight were used.
[3]Populations re-equalized after accidental mortality from temporary relocation of fish.
[4]New fish added for genetic variability.

sufficient genetic variability might exist in the populations to permit a genetic effect of selection. Since one of the major objectives of the experiment was to detect such an effect, I decided to add outside stock. During the 2-mo period preceding month 47.3 (Table 3), I added 45-47 (2 fish uncertainty due to counting difficulties) immature *Tilapia mossambica* from Arizona to each population. These fish were descendants of ones from Malacca.

Exploitation was started at month 39.2 (Table 3, Figures 1, 2) at a conservative 10% per 2 mo. This exploitation period included 1.0 to 2.6 of the brood intervals reported by various authors (Kelly 1957, 30-40 days; Swingle 1960, 30-40 days; Uchida and King 1962, 23-61 days). Because of irregularities in recruitment, population numbers (Figure 1) reflected population responses less well than population biomasses (Figure 2). The latter, however, generally reflected the expected population decrease from imposition of the 10% exploitation rate. When the rate was increased to 20% at month 63.2 (Table 3, Figure 2), further declines in population biomasses occurred.

BASIC RELATIONS

Recruitment was estimated from changes (R_{INT}) in stock number and data of mortality and catch (Table 4), using the approach of Silliman (1972). Because of variations in length of period between counts, values of R_{INT} were adjusted to a standard 2-mo interval (Table 4). Observation of large numbers of fry in the refuges, followed by the later appearance of peaks of recruitment (Table 4), indicated that the "reproductive lag" was about 2

TABLE 4.–Recruitment and stock. $R_{INT} = P_{n+1} - P_n + M_{INT} + C_{INT}$, where P is stock, INT is interval between counts n and $n+1$, R is net change[1], M is recorded mortality and C is catch, all in numbers. $\bar{S}$ is mean stock in kilograms for previous interval.

Interval (months)	Interval length (months)	Selectively fished population			Unselectively fished population		
		R_{INT}	[2]R_{INT}	$\bar{S}$	R_{INT}	[2]R_{INT}	$\bar{S}$
5.5- 7.5	2.0	−3	−3.0	1.4	+9	+9.0	1.1
7.5-10.5	3.0	+1	+0.7	2.6	+1	+0.7	2.4
10.5-13.0	2.5	+4	+3.2	4.4	−13	−10.4	4.5
13.0-15.0	2.0	+15	+15.0	6.5	+21	+21.0	6.5
15.0-17.1	2.1	−5	−4.8	7.8	−5	−4.8	8.0
17.1-19.2	2.1	−2	−1.9	8.8	−5	−4.8	9.0
19.2-21.1	1.9	0	.0	9.8	+19	+20.0	9.8
25.4-27.2	1.8	+25	+27.8	—[3]	−1	−1.1	—[3]
27.2-29.1	1.9	−1	−1.1	9.1	−1	−1.1	9.0
29.1-31.3	2.2	+9	+8.2	10.0	+6	+5.5	9.7
31.3-33.1	1.8	−6	−6.7	10.4	−12	−13.3	9.9
33.1-35.3	2.2	−2	−1.8	10.4	−2	−1.8	9.7
35.3-39.2	3.9	+44	+22.6	10.1	+16	+8.2	9.6
39.2-41.3	2.1	+7	+6.7	10.8	+10	+9.5	9.8
41.3-43.2	1.9	+4	+4.2	9.1	+30	+31.6	9.4
43.2-45.2	2.0	+8	+8.0	8.4	+30	+30.0	9.4
45.2-47.3	2.1	[4]+16	+15.2	8.2	[4]−6	−5.7	9.0
47.3-48.9	1.6	+2	+2.5	8.5	0	.0	9.1
48.9-51.2	2.3	+4	+3.5	8.8	−1	−0.9	9.4
51.2-53.2	2.0	−1	−1.0	9.2	−3	−3.0	10.0
53.2-55.1	1.9	+5	+5.3	9.2	+18	+18.9	9.4
55.1-57.2	2.1	+31	+29.5	8.8	0	.0	9.0
57.2-59.0	1.8	+3	+3.3	8.3	−1	−1.1	8.7
59.0-61.1	2.1	−2	−1.9	7.9	+2	+1.9	8.3
61.1-63.2	2.1	+5	+4.8	7.6	+73	+69.5	8.0
63.2-65.4	2.2	−1	−0.9	7.4	−16	−14.5	7.9
65.4-67.1	1.7	+3	+3.5	6.5	+15	+17.6	7.3
67.1-69.1	2.0	+199	+199.0	6.0	+75	+75.0	6.8
69.1-71.2	2.1	+62	+59.0	6.2	+6	+5.7	7.0
71.2-73.2	2.0	+16	+16.0	5.6	−1	−1.0	7.0
73.2-75.1	1.9	−2	−2.1	5.7	+1	+1.1	6.8

[1]$R_{INT} > 0$ indicates recruitment of at least the indicated number of fish; $R_{INT} < 0$ indicates unrecorded mortality of at least the indicated number and $R_{INT} = 0$ indicates either no recruitment and unrecorded mortality or the two exactly balanced.
[2]Adjusted to a standard 2-mo interval length.
[3]Indicated intervals omitted because of re-equalization of stocks.
[4]Exclusive of 46 new fish added for genetic variability.

mo. Each value of R_{INT} was therefore compared with the mean stock ($\bar{S}$) for the preceding 2-mo interval (Table 4).

The stock-recruitment data were highly variable and were, therefore, treated as group means based on 5-kg intervals of $\bar{S}$, considering negative values of R_{INT} to be equal to zero. Although the data indicated no regular relation (Figure 3), they were fitted with parabolas to indicate central tendency, even though fits were poor. These, based on 30 pairs of observations each, were:

Selectively fished stock

$$R_{N+1} = 6.163\ \bar{S}_N - 0.5209\ \bar{S}_N^2.$$

Unselectively fished stock

$$R_{N+1} = 3.304\ \bar{S}_N - 0.2158\ \bar{S}_N^2,$$

where N is number of the 2-mo interval, R is in

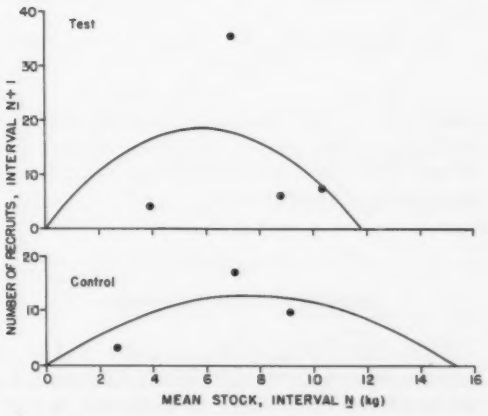

FIGURE 3.–Stock and recruitment. Test population was selectively fished; control, unselectively. Parabolas shown were fitted by least squares.

numbers, and S is in kilograms. The somewhat higher maximum for the selectively fished stock may have resulted from its changed size composition; it included fewer extremely large males than the unselectively fished population.

Since selection reflected the ability of fish to escape through vertical slots between glass bars, thickness was the controlling dimension. Most of the fish-size data in this report are therefore in thickness. However, to reduce fish handling to a minimum, the growth measurements of live fish during the final part of the experiment were in lengths. Because of this, and because other biologists may wish to compare their length data with my thickness data, I calculated thickness-length relations.

Measurements for the relation were from the caught fish, for which both thickness and length were recorded. Preliminary analysis showed that data for immature and male fish could be combined into a single rectilinear regression of length on thickness. The regression for females was also rectilinear but had a gentler slope, probably because of the distention of mature fish carrying eggs. It was therefore calculated separately. The regression equations, numbers of pairs of observations in parentheses, and correlation coefficients were (fitting was by least squares):

Immature and male

$$L = 7.027\,T \qquad (368) \qquad r = 0.987 \qquad r^2 = 0.974.$$

Female

$$L = 26.89 + 5.037\,T \qquad (207) \qquad r = 0.866$$
$$r^2 = 0.750,$$

where L is length and T is thickness, both in millimeters. The squared coefficients suggest that 97 and 75% of variations in length were associated with variations in thickness.

RESULTS

Exploitation and Response

Before selective exploitation could be started, it was necessary to determine the selection point. To aid in this the thickness of all of the fish in both populations was measured at month 33.5. At this time the population to be selectively fished (pretest) consisted of 85 males and 95 females—that to be unselectively fished (precontrol), 77 and 98, respectively. The thickness frequencies (Figure 4) revealed a low point in the pretest population between males and females at about 25 mm. This was used as the initial selection point and it meant, of course, that the early catches were mostly males. It will be shown below, however, that later catches were composed of roughly equal proportions of males and females.

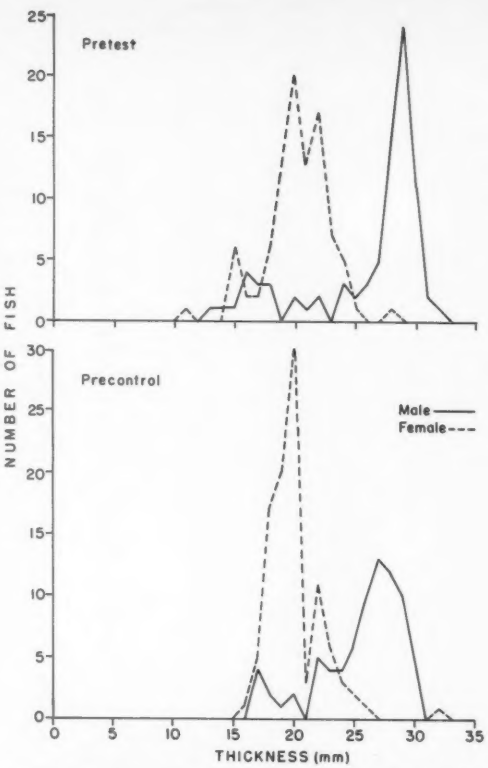

FIGURE 4.—Thickness frequencies at month 33.5. Test population was to be selectively fished; control, unselectively.

Changes from exploitation, in addition to those described under "Course of Populations," were reflected in the size composition of the catches (Figures 5, 6). In the test population, the catches were roughly the target percentage of the selected group; the percentages in the control population were adjusted to take the same proportion of the entire population as taken in the test population. Percentages were by number at months 39.2 and 41.3, but it became evident that this procedure took too large a proportion of the biomass. At months 43.2-75.1, the percentages were by weight

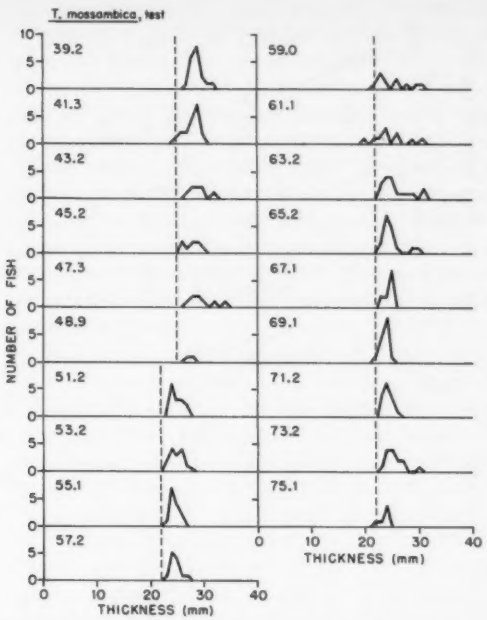

FIGURE 5.—Bimonthly thickness frequencies of catches, test (selectively fished) population. Vertical broken lines indicate selection points. Numbers in panels indicate months from start.

(Table 3). Numbers of fish growing above the selection point rapidly diminished in the test population (Figure 5) so that insufficient numbers were available from which to catch the target percentage. To continue exploitation, it was necessary to lower the selection point to 22 mm as shown. With few exceptions, all fish caught from the test population were above the selection point.

Catches from the control population were taken representatively over all sizes larger than fry and, therefore, represented the size composition of the stock above the fry size (Figure 6). Significant amounts of recruitment at months 43.2, 45.2, 55.1, 63.2, 67.1, and 69.1 (Table 4) appear as modes of small fish in the size frequencies, and the more prominent ones can be traced through succeeding frequencies.

A summary of catch size frequencies (Figure 7) clearly reveals the differences between catches from test and control populations. It is evident that the selection device employed was almost completely effective. The appearance of roughly equal proportions of males and females in the test catches, after lowering the selection point, is also apparent. It can be seen that a selection curve was at work, such that fish were not fully retained until they had reached a thickness of about 2-4 mm above the selection point.

The relation of yield to exploitation was assessed by fitting a Fox (1970) exponential surplus-yield model to data of catches and stock (Figure 8). The method of fitting used requires equilibrium yields. Although absolute equilibrium obviously was not attained, it was considered that the biomass and catch levels (Figure 2) at months 29-35 (zero exploitation), 59-61 (10% target rate), and 69-73 (20% target rate) represented sufficiently close approximations to equilibrium for fitting the model. The calculated maximum sustainable yield (1.39 kg per 2 mo) from the selectively fished test population was substantially lower than that for the unselectively fished control (2.36 kg). If we wish to consider a comparable commercial fishery, however, we might assume that only the fish above the selection point are commercially desirable. Catch thickness frequencies for the 22-mm selection point (Figure 7) showed that 97% of the fish in test catches were above the selection point as compared with 40% for the control catches. Although these data cannot be

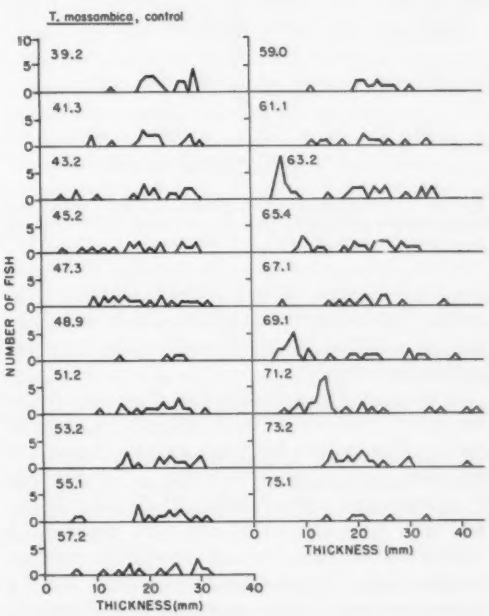

FIGURE 6.—Bimonthly thickness frequencies of catches, control (unselectively fished) population. Numbers in panels indicate months from start.

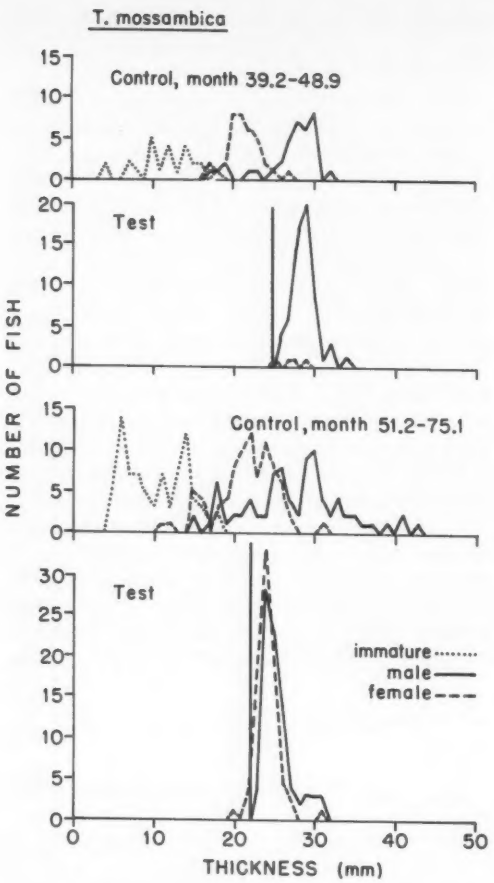

FIGURE 7.—Summary of catch thickness frequencies. Test population was fished selectively; control, unselectively. Vertical lines indicate selection points.

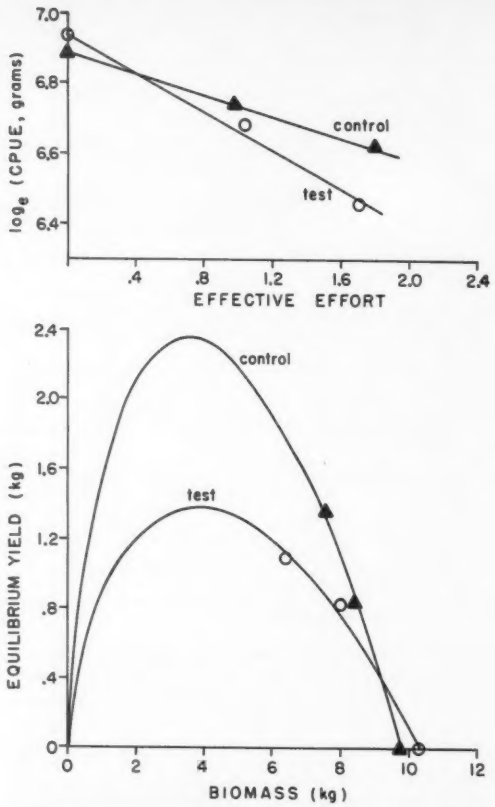

FIGURE 8.—Fitting of Fox (1970) model. Catch-per-unit-effort (CPUE) is considered proportional to biomass; effort is in arbitrary units. Regression lines shown are least-squares fits. Target exploitation rates were 0, 10%, and 20% per 2 mo, left-to-right in upper panel, reversed in lower panel.

converted to weights, it is certain that the comparison for fish above the selection point would be more favorable to the test catches than was true for all sizes of fish.

It is possible to calculate the efficiency of conversion of food to fish flesh under both types of fishing. The amount fed per 2-mo period was 3.75 kg (433 g per week from Table 1, for 8⅔ wk). Maximum sustainable yields (MSY's) of 1.39 kg and 2.36 kg indicate 37 and 63% conversion efficiencies for selective and unselective fishing, respectively. Since the theoretical MSY's represent a considerable extrapolation (Figure 8), it is of interest to calculate from equilibrium yields actually attained during the experiment. The largest yields were under the 20% per 2-mo target rate for both populations. Effective exploitation rates and corresponding yields were: selectively fished, 17.1% and 1.09 kg; unselectively fished, 17.9% and 1.35 kg. These yields indicate 29 and 36% efficiency, respectively. The values are in fair agreement with the 33% calculated by Silliman (1970) for the initial growth of the populations.

Genetic Response

Knowledge of the number of generations involved is essential to any genetic experiment. Progression of the two most prominent thickness frequency modes (months 63.2 and 69.1) in the unselectively fished population (Figure 6) gave an indication of the growth rate of the fish. Frequen-

cies of thickness for immature and mature fish (Figure 7) suggested a thickness at maturity of about 15-20 mm. The two prominent modes in the frequencies seemed to require about 4 mo (63.2-67.1, 69.1-73.2) to reach this size. To this must be added the 2-mo "reproductive lag" mentioned above under "Basic Relations," suggesting a generation length of about 6 mo. The 36-mo period of selective fishing would thus include about six potential generations. Because of irregularities in recruitment, however, the effective number of generations was less, and it was necessary to make an estimate.

Such an estimate can be derived from the record of recruitment numbers (R_{INT}, Table 4, Figure 9). An arbitrary criterion for significant recruitment was established, requiring at least 15 recruits per 2 mo. A generation was considered to be such a peak separated from the previous filial generation by a period of at least 6 mo (the parental generation for the test group had been fished selectively at month 40). Under the arbitrary criterion the estimated generations (Figure 9) during the selection period were only three for the selectively fished test and four for the unselectively fished control population. Experiments with other animals, such as those of Robertson with thorax length of *Drosophila* cited by Falconer (1960), have shown that measurable change in a size character can occur in as few as three generations of selection.

To test whether genetic response to selection did occur, groups of 46 mature fish as similar in sex and length composition as possible were selected from test and control populations on 5 January 1973 at month 77.2 (Table 5). It was not possible to match these fish as closely as desired by total weight, and that of the control group exceeded that of the test group by 19%. These fish were fed the standard diet (Table 1) which furnished them, even at the end of the growth period, with 1.5% (test) or 1.3% (control) of body weight of food per day. This was 2.5 (test) or 2.1 (control) times as much as was received by the 10 kg preexploitation stocks. Any offspring that appeared were removed as soon as possible.

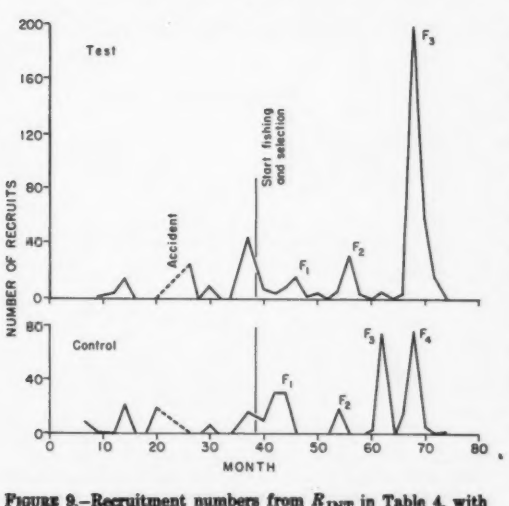

FIGURE 9.–Recruitment numbers from R_{INT} in Table 4, with negative values considered zero. Test population was selectively fished; control, unselectively.

TABLE 5.–Growth of selected groups of fish. Lengths are from snout to tip of tail.

Group	Day[1]	Male No.	Male Mean length (mm)	Female No.	Female Mean length (mm)	Total No.	Total Wt. (g)
Test	0	10	152.0	36	140.6	46	2,158
	56	[2]9	180.0	[2,3]36	155.0	45	3,199
	118	9	197.8	[4]34	165.0	43	3,794
	150	9	207.2	[3]33	169.8	42	4,078
Control	0	10	148.0	36	141.4	46	2,561
	55	[5]8	195.0	[3,5]37	153.4	45	3,504
	119	8	235.6	[6]35	164.4	43	4,455
	151	8	253.1	[7]34	169.1	42	4,819

[1]0 = 5 January 1973.
[2]One female misclassified as male on day 0.
[3]One female died.
[4]Two females died.
[5]Two females misclassified as males on day 0.
[6]Two females removed to match mortalities in test group.
[7]One female removed to match mortality in test group.

Growth of the selected fish was measured by determining the lengths of individual fish and the total weight of each group at 55-56, 118-119, and 150-151 days after the start of the growth period (Table 5, Figures 10, 11). The length frequencies reveal the general correspondence of the groups at the beginning of the period, in addition to the expected more rapid growth of the males than the females in each group. They also reveal that the males in the unselectively fished control group grew more rapidly than those in the selectively fished test group.

Growth was further studied by curves based on mean lengths and total weights of the selected groups. Gompertz curves fitted to lengths had the equation:

$$L_{t'} = L_0 \exp[G - G \exp(-gt')],$$

where L is mean length in millimeters, t' is time in days, and G and g are empirical constants. This curve and all other Gompertz curves were fitted by

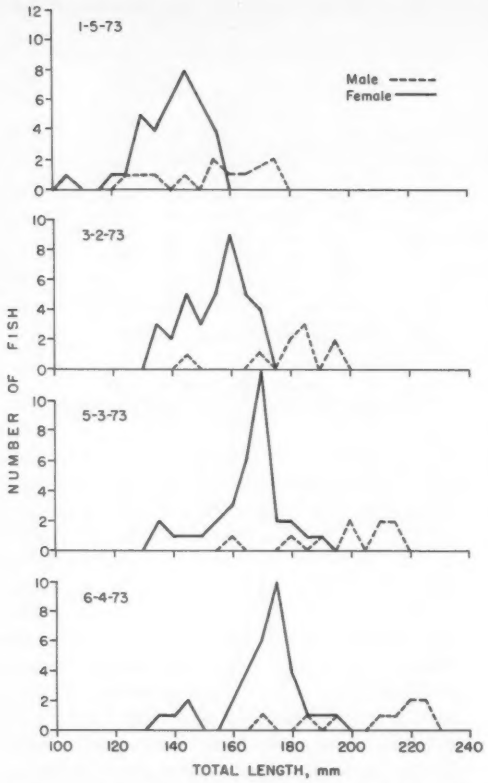

FIGURE 10.—Length frequencies of group selected from selectively fished test population. Lengths are from snout to tip of tail.

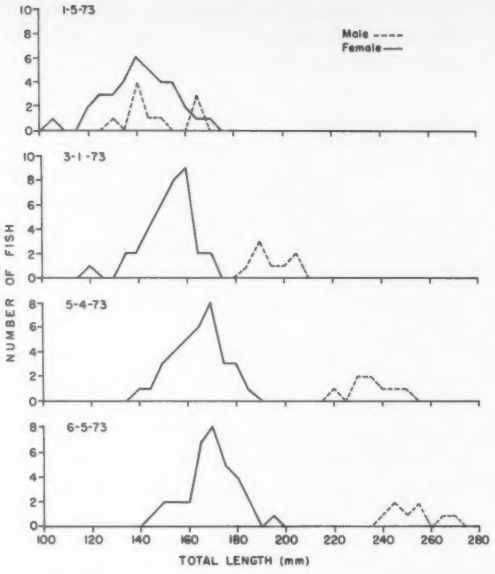

FIGURE 11.—Length frequencies of group selected from unselectively fished control population. Lengths are from snout to tip of tail.

the analog computer method of Silliman (1967). Growth in length was essentially identical in the two groups for the females (Table 5, Figure 12), and a single curve was fitted. Constants are given in Table 6. For males, however, growth was significantly greater in the unselectively fished control group than in the selectively fished test group.

The sexual misclassification of one fish in the test group and two in the control group (Table 5) must be considered in relation to possible effects on the results. These fish were misclassified at the beginning of the growth period, when the fish were relatively small (chosen so to provide room for growth) and sex determination was difficult. As the fish grew and determination became easier, the errors were discovered and corrected. To test the effect of the errors it was assumed that they occurred in the manner most contrary to the conclusion adopted—that growth was greater among males in the control than in the test group.

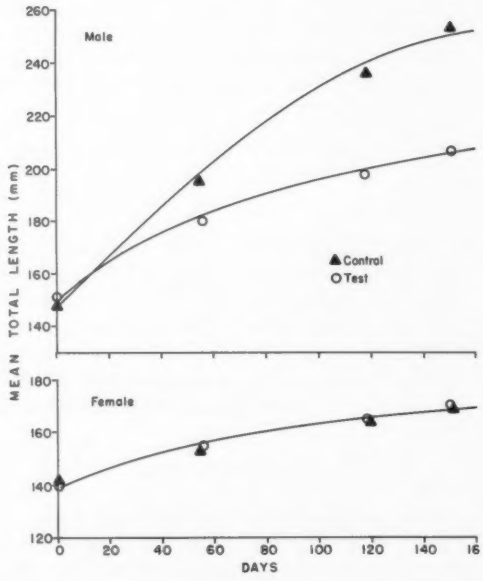

FIGURE 12.—Gomperts curves fitted to mean lengths in group selected from selectively fished test population and unselectively fished control population.

TABLE 6.–Constants of Gompertz curves for growth of selected groups of fish.

Sex	Variable	Population	L_0 (mm)	L_∞ (mm)	W_0 (kg)	W_∞ (kg)	g	G
♂	Length	Test	148	214	—	—	0.0150	0.367
		Control	146	274	—	—	0.0127	0.630
♀	Length	Both	141	174	—	—	0.0128	0.211
Both	Weight	Test	—	—	2.23	4.45	0.0130	0.692
		Control	—	—	2.49	5.65	0.0105	0.819

Note: L_0 = Length at time zero.
L_∞ = Asymptotic limit of length.
W_0 = Weight at time zero.
W_∞ = Asymptotic limit of weight.
g and G = Empirical constants of the Gompertz curve.

Thus it was assumed that at day 0 one of the two males at maximum length in the test group was misclassified as a female and, similarly, for the two smallest males in the control group. Resulting mean lengths in millimeters comparable to those for day 0 in Table 5 are: test male, 149.4; test female, 141.5; control male, 151.2; control female, 141.1. Percentage differences are 1.7, 0.6, 2.2, and 0.2, respectively. The means under the "most contrary assumption" are indistinguishable from the values used on the scale of Figure 12. It is evident that substitution of the most contrary values would not change the conclusion of greater male growth in the controls.

Gompertz curves were also fitted to biomasses of the two groups (Table 5, Figure 13). Here the equation was:

$$W_{t'} = W_0 \exp[G - G \exp(-gt')],$$

where W is total weight in kilograms, t' is time in days, and G and g are empirical constants. Constants are given in Table 6. In weighings, fish were not separated as to sex, and only a single growth curve was available for each population. Because of the initial difference in total weight, the curve for the control population is shown moved over to the time when weight of the test group had grown to the initial weight of the control group. Even so treated, the control group exhibits markedly greater growth than the test group, reflecting greater growth of the males in it. This is even more striking when it is considered that the amount of food per weight of fish was somewhat less in the control than in the test group. The observed growth in biomass supports the conclusion of diminished genetic growth in males as a result of selective fishing.

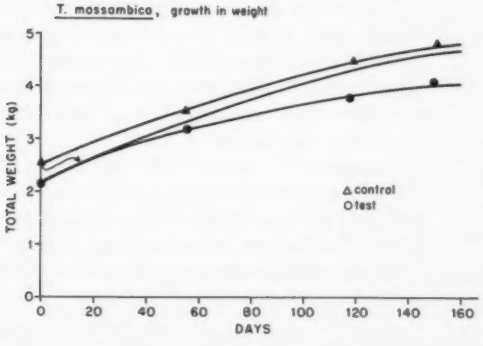

FIGURE 13.–Gompertz curves fitted to total weights of groups from selectively fished test population and unselectively fished control population. Line branching upward from test curve indicates control curve moved over to same starting point as test curve.

CONCLUSIONS

Analyses presented above have revealed significant differences of responses to exploitation between the selectively fished test population and the unselectively fished control population. These differences were demonstrated both in catches obtained and in genetic growth patterns.

Yield models fitted demonstrated marked differences in the catches obtained under selective and unselective fishing. It is clear that, with the particular populations studied and under the assumptions of stability made, weight of yield under unselective fishing was greater than that under selection. This yield included a large proportion of fish below the selection point, however. To the extent that one may generalize from this experiment, it appears that unselective fishing would be preferable if maximum physical yield were the sole objective. If selection is required to secure fish that are of appropriate size for the market, the objective may be achieved only at the sacrifice of part of the weight of the catch.

That three generations of selective fishing caused a change in the genetic growth pattern of males, resulting in slower growth than in the controls, seems certain from the results. It is necessary to explain, however, why a similar change did not occur in the females. This may have resulted from the phenomenon of epistasis. In this it is considered that a single gene may control the hormone which permits males to grow to larger ultimate size than females. Since females have less of this hormone than males, they are unable to

express genotypic differences which otherwise might cause changed growth patterns. In other words, the degree of selection imposed did not work against females because they were unable to achieve extra large size in any event. This hypothesis cannot be tested with data from the present experiment.

Fishing in the experiment was similar to that in a commercial fishery, with the vertical slots in the apparatus corresponding to the meshes of commercial gear. Results may, therefore, be of some significance in fishery management. They suggest that as wide a range of sizes as possible be included in the catch. An appropriate balance should be struck between the possible higher market value of large fish and the lesser yields that may be achieved under selection. Also, the possibility of a genetic change in growth pattern under selection should not be overlooked.

SUMMARY

1. Two populations of *Tilapia mossambica* were grown with as nearly identical space, water condition, and food as possible.
2. After a period of initial growth each population stabilized at a weight of about 10 kg. Numbers were less stable at this time and ranged from 173 to 218 fish.
3. To increase genetic variability, 45-47 immature fish of Malacca descent were added to each population at month 47.3.
4. Exploitation was started at month 39.2, at 10% per 2 mo (1.0-2.6 brood intervals) and increased to 20% at month 63.2. Selective fishing was from fish which could not pass through 25-mm (later 22-mm) vertical slots between glass rods. Unselective fishing was from all fish except fry (under 4-mm thickness).
5. Recruitment was estimated from data of stock number, mortality, and catch. Reproductive lag was 2 mo. The stock-recruitment relations, roughly fitted with parabolas, suggested greater recruitment in the selectively fished stock than in the unselectively fished one.
6. Two rectilinear thickness-length relations were calculated, one for immature and male fish and another for females.
7. Catch thickness frequencies for the unselectively fish population revealed modes corresponding to peaks of recruitment.
8. Catch thickness frequencies for the selectively fished population, compared with those for the unselectively fished population, demonstrated that the device for selection at 25 and 22 mm was almost completely effective.
9. The exploitation-yield relation was assessed by fitting Fox exponential surplus-yield models to data from both populations. Fitted models indicated a higher maximum sustainable yield in weight for the unselectively fished population than for the selectively fished one. Efficiency of food conversion was 29-36%.
10. Growth rates from catch thickness frequencies, together with the 2-mo reproductive lag, suggested a generation length of 6 mo. Recruitment records indicated three generations under exploitation for the selectively fished population and four during the same period for the unselectively fished one.
11. To test for genetic effect of selection, a group of 46 fish was selected from each population. These were matched as closely as possible by size and sex composition and grown under previously established standard conditions.
12. Growth in length over a period of 150 days was significantly greater among males from the unselectively fished population than among males from the selectively fished one. Growth for females in the two groups was practically identical.
13. Growth in total weight was distinctly greater for the group from the unselectively fished population than in that from the selectively fished one.
14. It was concluded that these experiments demonstrated diminished total yield and retarded male growth in the selectively fished population compared with the unselectively fished one. An hypothesis based on epistasis was advanced to explain lack of growth response among females.
15. As applied to commercial fisheries, the experimental results suggest fishing as wide a range of sizes as possible. If economic gains from selection are indicated, they should be balanced against possible costs in reduced total yield and retarded growth rate.

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LITERATURE CITED

FALCONER, D. S.
1960. Introduction to quantitative genetics. Ronald Press, N.Y., 365 p.

FOX, W. W., JR.
1970. An exponential surplus-yield model for optimizing exploited fish populations. Trans. Am. Fish. Soc. 99:80-88.

KELLY, H. D.
1957. Preliminary studies on *Tilapia mossambica* Peters relative to experimental pond culture. Proc. 10th Annu. Conf. Southeast Assoc. Game Fish Comm., p. 139-149.

LEWIS, W. M.
1963. Maintaining fishes for experimental and instructional purposes. South.Ill. Univ. Press, Carbondale, Ill., 100 p.

MILLER, R. B.
1957. Have the genetic patterns of fishes been altered by introductions or by selective fishing? J. Fish. Res. Board Can. 14:797-806.

ST. AMANT, J. A.
1966. Progress report on the culture of *Tilapia mossambica* (Peters) hybrids in southern California. Resour. Agency Calif. Dep. Fish Game, Inland Fish. Adm. Rep. 66-9, 25 p.

SILLIMAN, R. P.
1967. Analog computer models of fish populations. U.S. Fish Wildl. Serv., Fish. Bull. 66:31-46.
1970. Growth in experimental populations of *Tilapia mossambica*. BioScience 20:1109-1110.
1972. Effect of crowding on relation between exploitation and yield in *Tilapia macrocephala*. Fish. Bull., U.S. 70:693-698.

SWINGLE, H. S.
1960. Comparative evaluation of two tilapias as pondfishes in Alabama. Trans. Am. Fish. Soc. 89:142-148.

UCHIDA, R. N., AND J. E. KING.
1962. Tank culture of *Tilapia*. U.S. Fish Wildl. Serv., Fish. Bull. 62:21-52.

UPTAKE AND LOSS OF PETROLEUM HYDROCARBONS BY THE MUSSEL, *MYTILUS EDULIS*, IN LABORATORY EXPERIMENTS

ROBERT C. CLARK, JR., AND JOHN S. FINLEY[1]

ABSTRACT

Petroleum paraffin hydrocarbons (n-$C_{14}H_{30}$ to n-$C_{37}H_{76}$) from No. 2 and No. 5 fuel oils were rapidly incorporated into the mussel, *Mytilus edulis*, in a laboratory system that simulated tides. The mussels were exposed to levels of petroleum hydrocarbons from a surface slick similar to those encountered in the environment after an oil spill. After 14 days in clean seawater, the mussels had lost most of the hydrocarbons from the fuel oils; however, detectable traces of the No. 2 fuel oil still remained after 35 days. Preliminary results from these laboratory studies confirm previous studies of pollutant uptake and loss following actual oil spills.

Petroleum hydrocarbon uptake by the common bay mussel, *Mytilus edulis*, can be readily determined in the laboratory with the analytical chemical methods of solvent extraction, liquid-solid, and gas-liquid chromatography. Mussels lend themselves well to such studies because of 1) their worldwide distribution and ready availability (Davies 1969; Becker et al. 1973); 2) the considerable amount of physiological base line data available (Field 1922); 3) their hardiness as an experimental test organism (Gilfillan 1973); 4) their convenient size, which is small enough to sample adequately and use in the laboratory experimentally but large enough for specific organ dissection (Lee, Sauerheber, and Benson 1972); 5) their position in the intertidal ecosystem as a major pathway for energy transfer utilizing phytoplankton and debris (Ricketts and Calvin 1962); and 6) their known capacity for concentrating various pollutants from their environment (Greffard and Meury 1967; Modin 1969; Zitko 1970; Clark and Finley 1973a).

Earlier studies of hydrocarbon uptake and its effects on marine organisms include those by Griffith (1970) who determined the toxicity of Arabian light crude oil and oil-dispersant mixtures on mussels under tidal conditions, and Lee, Sauerheber, and Benson (1972) who used mineral oil and radio-labeled [^{14}C] heptadecane to study the laboratory uptake, body distribution, and loss of hydrocarbons in mussels. We previously reported on uptake of petroleum hydrocarbons by aquatic organisms from several oil spills (Clark and Finley 1973a). This paper reports the findings of a preliminary laboratory study using two refined petroleum products, a No. 2 fuel oil and a No. 5 fuel oil, in a laboratory system that simulates tidal action.

EXPERIMENTAL METHODS

A tidal aquarium for laboratory studies of the uptake and loss of petroleum by intertidal organisms has been described (Clark and Finley in press) (Figure 1). This system consists of two aquaria set at a 25° angle to represent a beach surface. The first aquarium contained the organisms being exposed to the pollutant, and the second aquarium, where all procedures were duplicated except for the pollutant exposure, contained control organisms. These control organisms served as the base line comparison for mortality studies and hydrocarbon analysis. The flood tide was simulated twice a day by pumping an artificial seawater medium (LaRoche et al. 1970) from a carboy using a timer-equipped, variable-speed pump. The ebb tide was accomplished by siphoning the seawater medium back into the carboys from beneath the surface oil slick in the test tank. Prior to exposure, the mussels (collected in an area distant from known sources of petroleum pollution) were acclimated to the tidal system for 24 h following a previous 48- to 96-h conditioning in the laboratory in an aerated aquarium (Table 1).

In practice, usually two sets of test organisms were used; one set was placed in the intertidal zone, held by glass rods placed horizontally across

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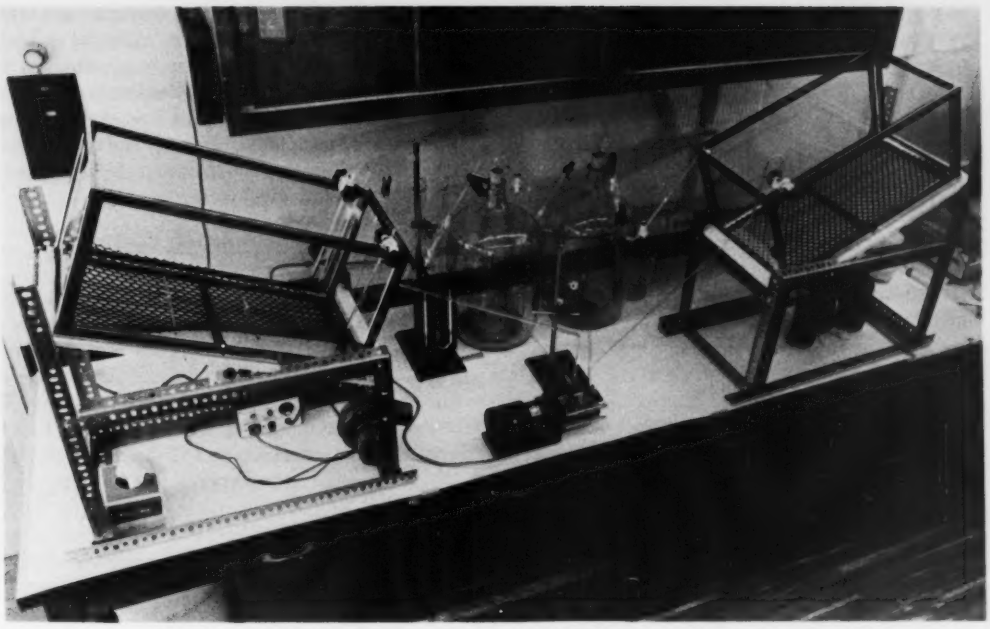

FIGURE 1.—Tidal aquarium system showing the test and control tanks.

the bottom of the sloping aquarium bottom, and exposed to the tidal sweep of the oil floating on the water surface. The second set was placed below the extreme lower level of the tidal sweep so that the organisms were continuously immersed in the medium where they were exposed to dissolved and emulsified fractions of the pollutant but never physically covered with oil.

During the experiment, a known volume of oil was layered onto the 1,700 cm^2 surface of the test aquarium at "high" tide. The system was then allowed to run through several complete tidal cycles in an attempt to simulate the conditions which might be found under a pier or along a beach following a significant oil spill. Two types of refined products were used in the uptake studies, a No. 2 heating fuel oil and a No. 5 heavy burner fuel oil.

TABLE 1.—Data on size of mussels, number of specimens, and experimental conditions.

Item	No. 2 fuel oil	No. 5 fuel oil
Average shell length	56.7 mm	54.7 mm
Number of specimens:		
Controls	36	16
Exposed — Surface slick	18	18
Exposed — Submerged	18	6
Exposure time	48 h	32 h
Complete tidal cycles	4	2.7
Water/air temperature	21°C	20°-22°C
Actual volume of oil applied	100 ml	97 ml
Slick thickness calculated:		
"High tide"	0.55 mm	0.53 mm
"Low tide"	1.53 mm	1.49 mm

At the end of the exposure, the bulk oil was skimmed from the surface at "high" tide, and the organisms were immediately placed in aerated aquaria containing seawater medium. The water was changed daily and the mussels fed a clam-based diet three times a day (LaRoche et al. 1970). Groups of the two sets of mussels were removed from these aquaria for analysis 1, 7, 14, and 35 days after the end of the exposure experiments.

The paraffin hydrocarbon analysis techniques for marine organisms have been described by Clark and Finley (1973b). Mussels were sampled and analyzed in groups of two to six individuals; analysis was run on the combined tissue and body fluids. No hydrocarbon content of the test seawater medium nor of the clean seawater was determined. Care was taken to minimize contamination of the shucked meats from oil that might have adhered to the shell, particularly in the early samples (1 and 7 days). All results have been reduced to "parts-per-million (ppm) dry extract-

ed-weight" basis (10^{-6} g of *n*-paraffin hydrocarbon per gram of the sum of the dried residue plus the solvent extractables).

RESULTS

Mortality Studies

Acute toxicity studies were not intended to be a major portion of this investigation since our paraffin hydrocarbon analysis techniques are used primarily on surviving organisms that have taken up oil pollutants at levels below that detectable by sight or smell.

The percentage of cumulative mortality (Figures 2 and 3) shows an approximate doubling for mussels exposed to the No. 2 fuel oil compared with the mussels exposed to the No. 5 fuel oil, although the duration of exposure was also greater for the No. 2 fuel oil (46 h vs. 32 h). Both the slick-exposed and the submerged specimens in the No. 5 fuel oil had a slightly higher mortality than the controls, but these differences might not be significant because of the small number of organisms used. The No. 2 fuel oil slick-exposed specimens, however, showed a mortality over twice that of the controls. The submerged specimens had a low initial mortality, but after 2 wk mortality had increased to the level of the slick-exposed specimens.

These mortality data provide a comparison of the two petroleum pollutants and of the test and control groups but were not further utilized to compute median tolerance limits which were beyond the scope and objective of these preliminary qualitative studies.

Griffith (1970) reported no mortalities in mussels exposed to aged crude oil for four tidal cycles over a total of 120 h. When the same mussels were placed in clean seawater, their rate of recovery was assessed by noting that byssal reattachment required 18 h for 50% of the exposed organisms but less than 12 h for the controls. No observations beyond 120 h (5 days) were reported.

No. 2 Fuel Oil Studies

Groups of mussels were collected 1, 7, 14, and 35 days after their removal to clean seawater medium. The *n*-paraffin hydrocarbon patterns for one set are presented as an example (Figure 4). If one assumes that the hydrocarbon pattern of the "controls" represents the natural or biogenic paraffin hydrocarbons and that the pattern of the "test" specimens represents the biogenic plus the pollutant, then by subtracting the former from the latter the resulting "residual" pattern might be expected to depict the pollution hydrocarbon pattern of the petroleum product tested. The "residual" paraffin patterns are shown for the No. 2 fuel oil bioassay study for mussels sampled 1 and 7 days (Figure 5) and 14 and 35 days (Figure 6) after removal from the pollutant.

The shape of the residual paraffin patterns for all four sampling periods approximates that of the pollutant below *n*-$C_{27}H_{56}$ and above a residual content level of 0.050 ppm., although individual paraffin hydrocarbons may show variation from the smooth, nearly bell-shaped curve for the No. 2 fuel oil. The quantities of uptake and loss of *n*-paraffin hydrocarbons from the No. 2 fuel oil by the mussels are shown in Figure 7. The uptake after

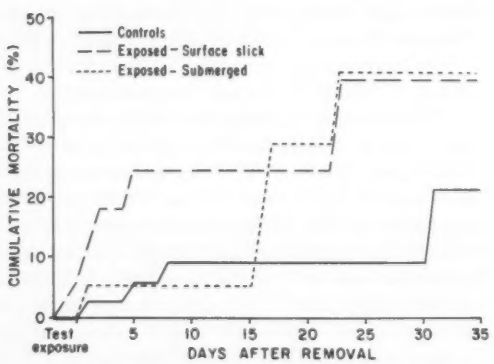

FIGURE 2.—Cumulative mortalities of mussels for 35 days following a 48-h exposure to a No. 2 fuel oil.

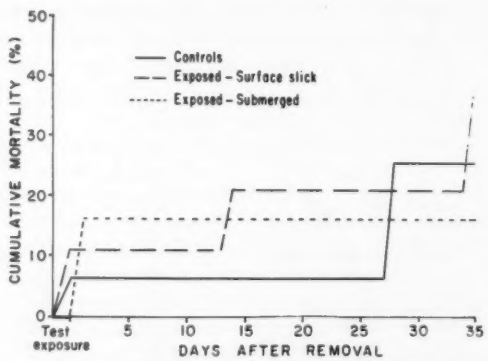

FIGURE 3.—Cumulative mortalities of mussels for 35 days following a 32-h exposure to a No. 5 fuel oil.

48-h exposure plus 1 day in clean medium was 110 ppm. for the slick-exposed specimens compared with only 29 ppm. for the submerged specimens. Within 7 days the residual content had dropped by nearly 75%, after which it declined at a slower rate but was still significantly above background (8 ppm.) after 35 days in the slick-exposed specimens.

No. 5 Fuel Oil Studies

The residual paraffin hydrocarbon pattern (Figure 8) for mussels exposed to a No. 5 fuel oil revealed a definite uptake of pollutant hydrocarbons at the end of the 32-h exposure, and the specimens collected 7 days later from clean seawater medium contained less than 1 ppm. total residual paraffin hydrocarbons attributable to the pollutant (Figure 7).

Gas-liquid chromatography of the saturated hydrocarbon fraction of the exposed mussels revealed a series of branched-chain hydrocarbons from below C_{14} to C_{26}, but of this series only pristane was quantified and included in the calculations. Most unsaturated and aromatic compounds were separated from the saturated fraction at the silica gel/alumina column chromatography stage without further analysis.

DISCUSSION AND CONCLUSIONS

These experiments, although preliminary in nature, provide four basic conclusions: 1) mussels rapidly took up pollution hydrocarbons during exposure; 2) mussels lost pollution hydrocarbons when removed from the test tanks and held in clean seawater (depuration), but significant quantities of No. 2 fuel oil remained for 35 days; 3) the *n*-paraffin residual pattern (exposed levels minus control levels) established for the exposed mussels nearly duplicated the shape of the pollutant hydrocarbon pattern; and 4) these laboratory results confirmed analyses made on shellfish following actual oil spills in the marine environment.

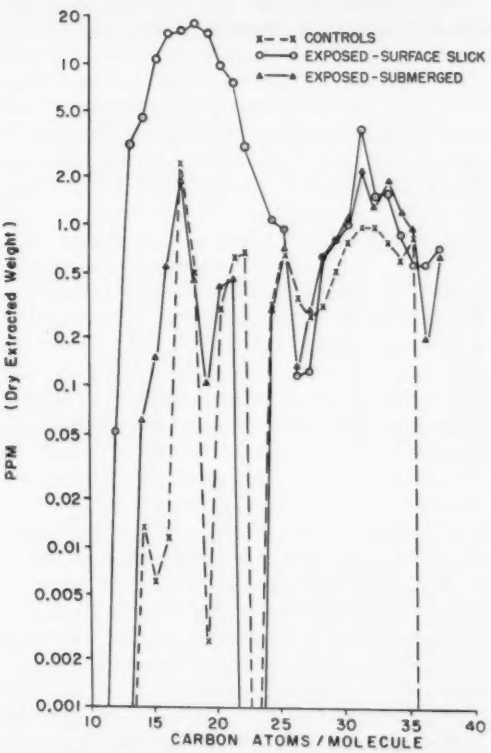

FIGURE 4.—Paraffin hydrocarbon patterns in mussels exposed to a No. 2 fuel oil: 1 day after removal.

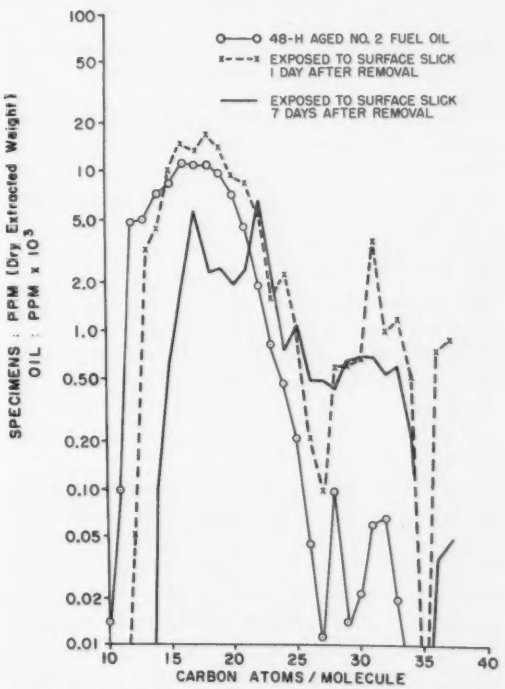

FIGURE 5.—Residual paraffin patterns of mussels exposed to a No. 2 fuel oil: 1 and 7 days after removal.

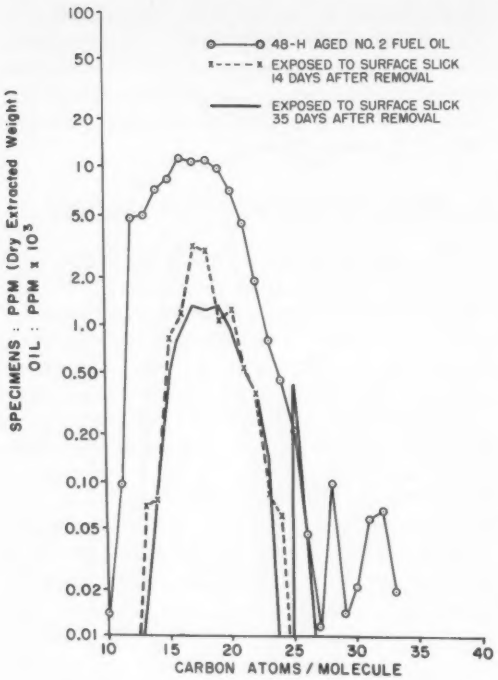
48-H AGED NO. 2 FUEL OIL
EXPOSED TO SURFACE SLICK 14 DAYS AFTER REMOVAL
EXPOSED TO SURFACE SLICK 35 DAYS AFTER REMOVAL
SPECIMENS : PPM (Dry Extracted Weight)
OIL : PPM x 10³
CARBON ATOMS / MOLECULE

FIGURE 6.—Residual paraffin patterns for mussels exposed to a No. 2 fuel oil: 14 and 35 days after removal.

The mussels rapidly took up a wide range of petroleum paraffin hydrocarbons. Lee, Sauerheber, and Benson (1972) had found this to be the case for mussels where [^{14}C] heptadecane was detected within 15 min. The level of hydrocarbons we found in our mussels exposed to No. 2 fuel oil represents less than maximum uptake because after exposure they were held 24 h in clean seawater before sampling. The No. 5 fuel oil specimens were collected immediately after their 32-h exposure to the oil, and extreme care was exercised to avoid contaminating the tissue with any oil adhering to the outside of the shell when shucking prior to extraction.

Griffith (1970) suggests that the attachment of the byssal threads by the mussel could be affected by the exposure to petroleum. The byssal attachment is made by means of a grooved foot, which is extended from the shell and placed in contact with the substratum. Glandular secretions of collagen mixed with phenolic protein run from the foot groove, become attached to the substratum, and during withdrawal of the foot undergo tanning by the action of polyphenoloxidase (Pujol 1967). It is

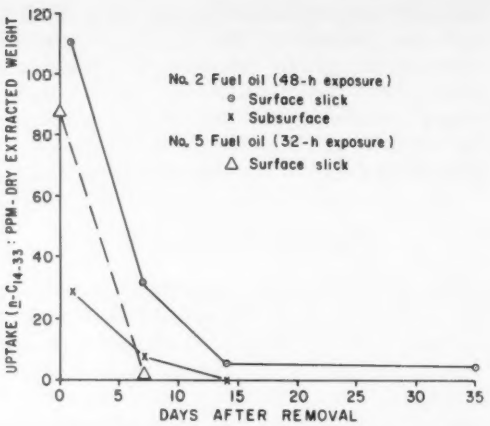

FIGURE 7.—*n*-Paraffin hydrocarbon uptake and loss of fuel oil by mussels.

not certain whether the oil upsets this chemical process or inhibits the muscular actions of the foot necessary to anchor the byssal thread.

When other mollusks such as the American oyster, *Crassostrea virginica*, were exposed to an

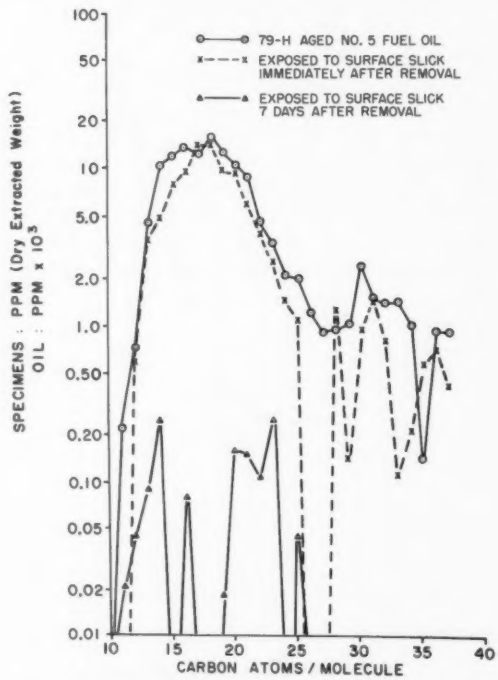
79-H AGED NO. 5 FUEL OIL
EXPOSED TO SURFACE SLICK IMMEDIATELY AFTER REMOVAL
EXPOSED TO SURFACE SLICK 7 DAYS AFTER REMOVAL
SPECIMENS : PPM (Dry Extracted Weight)
OIL : PPM x 10³
CARBON ATOMS / MOLECULE

FIGURE 8.—Residual paraffin patterns for mussels exposed to a No. 5 fuel oil.

oil-water mixture, as distinct from our nonagitated surface oil slick under tidal conditions, they also showed rapid uptake. Anderson (1973) found uptake of No. 2 fuel oil to be greatest in the first 24 h with lower uptake at longer periods. By comparison, he found uptake in clams, *Rangia cuneata*, reached a maximum in 72 h, and greater concentrations in the clam tissue were reached than for oysters. Aromatic hydrocarbons showed a greater uptake in the mollusk tissue than saturated forms.

Stegeman and Teal (1973), using a flow-through exposure system, showed that oysters initially took up a No. 2 fuel oil-water mixture in direct relation to the hydrocarbon concentration in the water up to at least 450 μg/liter, above which they remained closed. They also found an enrichment in aromatic fractions compared to the saturated fraction, and under long-term exposure (49 days) the latter fraction showed a progressive decrease in amount with increasing length of exposure.

Under our conditions the No. 5 fuel oil-exposed specimens took up less *n*-paraffin hydrocarbons than the No. 2 fuel oil-exposed mussels, and the former also lost them faster. Both sets of specimens had depurated their residual hydrocarbons by 75% within 1 week, but the No. 2 fuel oil-exposed mussels still contained detectable amounts at the end of 35 days. Lee, Sauerheber, and Benson (1972) found that mussels would discharge over 90% of the incorporated mineral oil after several days, a result they confirmed with labelled *n*-heptadecane.

Anderson (1973) found that oysters lost 94% of the saturated hydrocarbon uptake but only 82% of their aromatics after 13 days when exposed to a No. 2 fuel oil; after 52 days no residual pollutant hydrocarbons were detected at the 0.5-ppm. level (wet weight). Exposure to South Louisiana crude oil showed detectable but low levels of saturates but no detectable aromatics after 27 days depuration. Stegeman and Teal (1973) also found a rapid loss of hydrocarbons from oysters exposed to No. 2 fuel oil-water mixture, but a persistent portion (34 ppm. wet weight above background) remained.

These preliminary experiments did not provide results as to the mechanisms or pathways of petroleum hydrocarbon uptake by the contaminated mussels. The mechanisms of uptake and transport of pollutant hydrocarbons from the environment into organisms may have a very important effect on the degree to which the subsequent depuration is reversible. For instance, hydrocarbons transported across gill membranes in solution or as emulsified droplets enter the bloodstream of fishes very rapidly and can be rapidly depleted on removal of the pollutant (Roubal 1974). On the other hand, hydrocarbons in food sources are resorbed at a different site, which, for the basking shark occurs in the spiral valve where they are transferred to the liver and remain highly persistent (Blumer 1967).

The residual paraffin hydrocarbon patterns showed a strikingly similar pattern to the aged pollutant, yet the organisms appeared healthy and had no visible contamination or oily odor. Lee, Sauerheber, and Benson (1972) indicated that gas-liquid chromatograms of mineral oil in mussels were like the original mineral oil except for some loss of the short-chain paraffin hydrocarbons. Blumer et al.(1970) used gas chromatograms of oysters and scallops contaminated by a No. 2 fuel oil to show that the patterns had the same general features as the chromatogram of the fuel oil.

Anderson (1973) found an *n*-paraffin hydrocarbon pattern in clams similar to the high-aromatic No. 2 fuel oil; however, the maximum hydrocarbon in the clam (n-C_{17}: approximately 1.6 times more than n-C_{16} and 1.9 times n-C_{18}) was one carbon number higher than the pollutant maximum (n-C_{16}: 1.1-1.2 times the adjacent paraffins). Stegeman and Teal (1973) showed gas chromatograms of contaminated oysters having a pattern similar to the pollutant and a maximum *n*-paraffin concentration of C_{18} or C_{19}.

Our presentation of petroleum hydrocarbon uptake as evidenced by *n*-paraffin analyses is not a complete picture of petroleum contamination since it reflects only a portion of the total hydrocarbons and non-hydrocarbons in the oil. Also, the various hydrocarbon components of the petroleum are not necessarily available to the organisms in the water in the same proportion as they exist in the original petroleum. Vaughan (1973) reported an enrichment of methylnaphthalenes compared to n-$C_{12\text{-}20}$ paraffins of 15:1 in oysters exposed to a South Louisiana crude oil (50 μg/ml) in a seven-day bioassay experiment and an enrichment in the water extracts of about 3:1. Further, the *n*-paraffin content of petroleum pollutants in shellfish is often depleted with time relative to that of the source (Stegeman and Teal 1973). Therefore, while our values for pollutant uptake based on *n*-paraffin hydrocarbon analyses yield conservative estimates, they demonstrate that these experimentally simple methods can be

useful. Aromatic hydrocarbons, which are a biogenic rarity yet often a major component of petroleum and its refined products found to be rapidly taken up by marine organisms, may be rapidly lost from contaminated organisms (Lee, Sauerheber and Dobbs 1972; Stegeman and Teal 1973; Anderson 1973). Consequently, the utility of these compounds in marine pollution monitoring programs and in long-term bioassay experiments may be somewhat limited.

We previously reported (Clark and Finley 1973b) uptake by mussels, *M. edulis* and *M. californianus*, of petroleum *n*-paraffins following oil spills in the marine environment. A No. 2 fuel oil spill resulted in considerably greater uptake (10 ppm. of n-C_{17}) than for mussels exposed to Navy Special fuel oil residue (nearly 1 ppm. of n.-C_{17}); however, in both cases it was obvious that the apparently healthy mussels had acquired an *n*-paraffin hydrocarbon pattern like that of the pollutant. By creating an oil slick and a tidal system within an aquarium under laboratory conditions, it is possible to show that these earlier findings can be reproduced. These results add further support to the data of other investigators who used different approaches and analytical techniques.

We did not analyze hydrocarbon levels in specific organs, conduct metabolic studies, or determine aromatic content. Stegeman and Teal (1973) and Anderson (1973) found that aromatic hydrocarbons were often enriched in oysters in preference to the *n*-paraffins.

While we have given percentage loss of pollutant paraffin hydrocarbons in our presentation as well as actual concentration levels (Figure 7), the percentage value is very dependent on both the level of initial pollution exposure and on the lower limit of sensitivity of the experimental method for detecting pollutant uptake near biogenic background concentrations in marine organisms. Thus, one might have two sets of organisms showing similar concentrations of residual pollutant after considerable depuration but with a dramatically different percentage loss as a result of different exposure levels.

The variation of uptake and loss of petroleum hydrocarbons in marine organisms most certainly is related to the magnitude of the exposure—the amount of the pollutant and the duration, as well as physical and chemical properties of the pollutant.

LITERATURE CITED

ANDERSON, J. W.
1973. Uptake and depuration of specific hydrocarbons from oil by the bivalves *Rangia cuneata* and *Crassostrea virginica*. Background papers for A Workshop on Inputs, Fates and Effects of Petroleum in the Marine Environment, Airlie, Virginia, 21-25 May, Vol. II, p. 690-708.

BECKER, C. D., J. A. LICHATOWICH, M. J. SCHNEIDER, AND J. A. STRAND.
1973. Regional survey of marine biota for bioassay standardization of oil and oil dispersant chemicals. Am. Pet. Inst., Res. Rep., Publ. 4167, 106 p.

BLUMER, M.
1967. Hydrocarbons in digestive tract and liver of a basking shark. Science (Wash., D.C.) 156:390-391.

BLUMER, M., G. SOUZA, AND J. SASS.
1970. Hydrocarbon pollution of edible shellfish by an oil spill. Mar. Biol. (Berl.) 5:195-202.

CLARK, R. C., JR., AND J. S. FINLEY.
1973a. Paraffin hydrocarbon patterns in petroleum-polluted mussels. Mar. Pollut. Bull. 4:172-176.
1973b. Techniques for analysis of paraffin hydrocarbons and for interpretation of data to assess oil spill effects in aquatic organisms. Proceedings 1973 Joint Conference on Prevention and Control of Oil Spills, p. 161-172. Am. Pet. Inst., Wash., D.C.
In press. Tidal aquarium for laboratory studies of environmental effects on marine organisms. Prog. Fish-Cult.

DAVIES, G.
1969. Mussels as a world food resource. *In* F. E. Firth (editor), The encyclopedia of marine resources, p. 421-426. Van Nostrand Reinhold Co., N.Y.

FIELD, I. A.
1922. Biology and economic value of the sea mussel Mytilus edulis. Bull. U.S. Bur. Fish. 38:127-259.

GILFILLAN, E. S.
1973. Effect of seawater extracts of crude oil on carbon budgets in two species of mussels. Proceedings 1973 Joint Conference on Prevention and Control of Oil Spills, p. 691-695. Am. Pet. Inst., Wash., D.C.

GREFFARD, J., AND J. MEURY.
1967. Note sur la pollution en rade de Toulon par les hydrocarbures carcerigenes. Cah. Océanogr., Bull. Inf. Com. Cent. Océanogr. Étud. Côtes 19:457-468.

GRIFFITH, D. DE G.
1970. Toxicity of crude oil and detergents to two species of edible molluscs under artificial tidal conditions. FAO (Food Agric. Organ. U.N.) Tech. Conf. Mar. Pollut., Rome, December 1970, Pap. E-16, 12 p.

LAROCHE, G., R. EISLER, AND C. M. TARZWELL.
1970. Bioassay procedures for oil and oil dispersant toxicity evaluation. J. Water Pollut. Control Fed. 42:1982-1989.

LEE, R. F., R. SAUERHEBER, AND A. A. BENSON.
1973. Petroleum hydrocarbons: uptake and discharge by the marine mussel Mytilus edulis. Science (Wash., D.C.) 177:344-346.

LEE, R. F., R. SAUERHEBER, AND G. H. DOBBS.
1972. Uptake, metabolism and discharge of polycyclic aromatic hydrocarbons by marine fish. Mar. Biol. (Berl.) 17:201-208.

MODIN, J. C.
1969. Residues in fish, wildlife, and estuaries. Chlorinated

hydrocarbon pesticides in California bays and estuaries. Pestic. Monit. J. 3:1-7.

PUJOL, J. P.
1967. Formation of the byssus in the common mussel (*Mytilus edulis* L.). Nature (Lond.) 214:204-205.

RICKETTS, E. F., AND J. CALVIN.
1962. Between Pacific tides. 3rd ed., revised. Stanford Univ. Press, Stanford, 516 p.

ROUBAL, W. T.
1974. Spin-labeling of living tissue. *In* E. J. Vernberg (editor), Pollution and physiology of marine organisms, p. 367- 379. Academic Press, N.Y.

STEGEMAN, J. J., AND J. M. TEAL.
1973. Accumulation, release and retention of petroleum hydrocarbons by the oyster *Crassostrea virginica*. Mar. Biol. (Berl.) 22:37-44.

VAUGHAN, B. E.
1973. Effects of oil and chemically dispersed oil on selected marine biota—A laboratory study. Am. Pet. Inst., Publ. 4191, Wash., D.C., 105 p.

ZITKO, V.
1970. Determination of residual fuel oil contamination by aquatic animals. Bull. Environ. Contam. Toxicol. 5:559-564.

SYSTEMATICS AND MORPHOLOGY OF THE BONITOS (*SARDA*) AND THEIR RELATIVES (SCOMBRIDAE, SARDINI)[1]

BRUCE B. COLLETTE[2] AND LABBISH N. CHAO[3]

ABSTRACT

The bonitos constitute the scombrid tribe Sardini, consisting of eight species placed in five genera. They differ from the more primitive mackerels and Spanish mackerels in lacking a notch in the hypural plate and in having a bony lateral keel on the posterior caudal vertebrae. From the higher tunas, they differ in having the bony keel only incompletely developed and in lacking a specialized subcutaneous vascular system. The monotypic Australian endemic *Cybiosarda elegans* shares several characters with the monotypic eastern Atlantic endemic *Orcynopsis unicolor* (structure of the bony caudal keel; relative lengths of liver lobes; position and size of spleen) that distinguish them from *Gymnosarda unicolor* and the species of *Sarda*. *Sarda* contains four allopatric species, which differ from each other in such characters as numbers of fin rays, gill rakers, vertebrae, and teeth: the Atlantic *S. sarda*; the southeastern Australian *S. australis*; the tropical Indo-Pacific *S. orientalis*; and the eastern temperate Pacific *S. chiliensis*. The monotypic Indo-West Pacific reef species *Gymnosarda unicolor* is the only member of the Sardini that has a swim bladder and lacks intermuscular bones on the back of the skull. The monotypic Southern Ocean *Allothunnus fallai* differs from all other scombrids in having laterally extended prootic wings. It is more closely related to the bonitos than to any other scombrids. *Allothunnus* resembles the higher tunas in having a prootic pit but lacks the subcutaneous vascular system. Tables of meristic characters, diagrams of the soft anatomy, and drawings of most bones are included in the first part of the paper. The second part of the paper includes sections on synonymy, comparative diagnosis, types of nominal species, and distribution for each species.

The purpose of this paper is to clarify the relationships of the Sardini at the generic and specific level. This work is part of a continuing study of the systematics of the Scombridae. The methods used are similar to those used by Gibbs and Collette (1967) in a revision of *Thunnus* and rely heavily on the classic work of Kishinouye (1923) and Godsil (1954, 1955).

The bonitos (*Sarda*) and their relatives form a tribe (Sardini) of the subfamily Scombrinae intermediate between the primitive mackerels (Scombrini) and Spanish mackerels (Scomberomorini), and the more advanced tunas (Thunnini) (see Collette and Gibbs 1963a; Gibbs and Collette 1967). Five genera are treated in this paper. The status of the related monotypic genera *Orcynopsis*, *Cybiosarda*, and *Gymnosarda* has been unclear; for example, Fraser-Brunner (1950) placed *Cybiosarda* in the synonymy of *Gymnosarda*. The systematic position of the monotypic *Allothunnus* has been still more confused—whether it is closer to *Thunnus* (Fraser-Brunner 1950), to *Sarda* (Fitch and Craig 1964), or strikingly different from all other scombrids (Nakamura and Mori 1966). There has been no agreement on the number of species of *Sarda*. Fraser-Brunner (1950) recognized three species: *chiliensis*, *orientalis*, and *sarda*. Godsil (1955) believed that there were two basic groups of species—*sarda-chiliensis* and *orientalis-velox*. Some authors have considered *S. australis* as a valid species, others as a subspecies of *S. chiliensis*.

This project was initiated at the request of the FAO (Food and Agriculture Organization of the United Nations) panel of Experts for the Facilitation of Tuna Research at its Fourth Session in La Jolla, Calif. in November 1971, and should be considered as a report from the Working Party on Tuna and Billfish Taxonomy. Bonitos, as a group, are one of the few underexploited groups of tunalike fishes; therefore, research on their systematics is a necessary predecessor of successful management.

According to the FAO Yearbook of Fishery Statistics for 1972 (Food and Agriculture Or-

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ganization of the United Nations 1973), the two species of bonitos that are presently of economic importance are *Sarda chiliensis* and *S. sarda*. Peruvian fishermen landed 54,000-73,000 metric tons per year of the southeast population of *S. chiliensis* in 1965-1972. Smaller catches by Chile and of the northeast Pacific population by Mexico and the United States made the total 65,000-94,000 metric tons per year during that period. *Sarda sarda* is fished particularly by Turkey in the Mediterranean and the Black Sea where 11,700-55,200 metric tons per year were landed in 1965-1972. Other catches of *S. sarda* by Spain, Portugal, Greece, Angola, Argentina, and Brazil made the total 25,000-65,000 metric tons per year in 1965-1972. Both the Japanese and the Koreans fish for *S. orientalis* and there are smaller catches elsewhere throughout its range. *Sarda australis* comes into the markets in Sydney and probably elsewhere in southeastern Australia. In 1971, Morocco was reported to have landed 600 metric tons of *Orcynopsis* and we have seen *Orcynopsis* in the markets in Tunis. We have seen specimens of *Cybiosarda* in the Sydney fish market mixed with *S. australis*. The only commercial catch of *Allothunnus* was the 230 tons taken with purse seines off eastern Tasmania in June 1974 (Webb and Wolfe 1974). *Gymnosarda* occurs around coral reefs where it is taken by fishermen on hook and line.

Emphasis was placed on obtaining fresh or frozen specimens from each population of each species for dissection. Standard counts and measurements were taken, color pattern was recorded, and a search was made for parasitic copepods. Results of the copepod study will be reported on later by Roger F. Cressey (United States National Museum, USNM). The viscera were examined and drawn in situ following removal of an oval portion of the ventral body wall. The viscera were then removed and drawings were made of the liver and other selected organs. The kidneys and anterior parts of the arterial system were then drawn. Counts of ribs and intermuscular bones were made and the specimen was then skeletonized. Specimens were immersed in hot water to assist removal of the flesh.

For morphometric comparisons, the base measurement used for fresh, frozen, and preserved specimens was millimeters fork length (mm FL). Skeletal material was measured in millimeters skeletal length, the distance from the anterior margin of the ethmoid to the posterior tip of the hypural plate, a distance somewhat shorter than fork length. Skulls were measured from the anterior margin of the ethmoid to the posteroventral junction of the skull with the first vertebral centrum.

This paper is divided into two major sections. The first part describes and illustrates the squamation, morphometry, meristic characters, soft anatomy, and osteology of the Sardini. The second part treats the genera and species separately including synonymy, diagnosis (based on characters from the first section), types of nominal species, geographical distribution, and, for some species, geographic variation.

MATERIAL

Abbreviations used for the institutions cited herein are as follows:

AB - Northwest Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, Auke Bay, Alaska.
AMS - Australian Museum, Sydney.
ANSP - Academy of Natural Sciences, Philadelphia, Pa.
BMNH - British Museum (Natural History), London.
BPBM - Bernice P. Bishop Museum, Honolulu, Hawaii.
CAS - California Academy of Sciences, San Francisco.
CBL - Chesapeake Biological Laboratory, Solomons, Md.
CSIRO - CSIRO Marine Biological Laboratory, Cronulla, N.S.W., Australia.
DM - Dominion Museum, Wellington, New Zealand.
FMNH - Field Museum of Natural History, Chicago, Ill.
HUJ - Hebrew University, Jerusalem.
LACM - Los Angeles County Museum of Natural History, Los Angeles, Calif.
MACN - Museo Argentina de Ciencias Naturales, Buenos Aires.
MCZ - Museum of Comparative Zoology, Harvard.
MNHN - Muséum National d'Histoire Naturelle, Paris.
MSNG - Museo di Storia Naturale, Genoa.
MSUF - Museo de La Specola, Universita di Firenze, Florence.

NHMV - Naturhistorisches Museum, Vienna.
NMC - National Museum of Natural Sciences, Ottawa.
QM - Queensland Museum, Brisbane.
RMNH - Rijksmuseum van Natuurlijke Historie, Leiden.
RUSI - J. L. B. Smith Institute of Ichthyology, Rhodes University, Grahamstown.
SAM - South African Museum, Capetown.
SFRS - Sea Fisheries Research Station, Haifa, Israel.
SIO - Scripps Institution of Oceanography, La Jolla, Calif.
SMF - Senckenberg Museum, Frankfurt-am-Main.
TABL - Southeast Fisheries Center, National Marine Fisheries Service, NOAA (formerly Tropical Atlantic Biological Laboratory), Miami, Fla.
UBC - Institute of Fisheries, University of British Columbia, Vancouver.
UCLA - University of California, Los Angeles.
UMML - Rosenstiel School of Marine and Atmospheric Science, Miami, Fla.
UMMZ - University of Michigan Museum of Zoology, Ann Arbor.
USNM - United States National Museum, Washington, D.C.
WAM - Western Australia Museum, Perth.
WHOI - Woods Hole Oceanographic Institution, Woods Hole, Mass.
ZMK - Zoological Museum, Copenhagen.
ZMO - Zoological Museum, Oslo.

The material examined is listed by general locality under four or five headings for each species (except *Sarda chiliensis*, *S. orientalis*, and *S. sarda* which are subdivided into two populations each). The numbers in each category are not additive but are included to give some degree of confidence in the morphological data presented in the body of the paper. "Total specimens" is the total number of individuals examined whether preserved, dissected, or skeletons. "Measured and counted" includes specimens that were subsequently dissected and the preserved museum specimens used for detailed morphometric and meristic examination. "Counts only" are the additional museum specimens used only for meristic examination. "Skeletons" refer to all the skeletal material examined, specimens that were dissected plus skeletal museum material.

Allothunnus fallai. Total 8 specimens (451-787 mm FL).

Dissected 4 (680-778). Tasmania (3); California (1).

Measured and counted 7 (642-787). Tasmania (4); California (1); New Zealand (2).

Skeletons 5 (451-778). Tasmania (3); California (1); South Africa (1).

Cybiosarda elegans. Total 22 specimens (250-422 mm FL).

Dissected 5 (355-422). Perth, Western Australia (1); Macleay River, New South Wales (4).

Measured and counted 21 (250-422). New South Wales (11); E. Queensland (7, including holotype of *Scomberomorus* (*Cybiosarda*) *elegans* Whitley); Gulf of Carpentaria (1); Western Australia (2).

Examined 1 (380). New South Wales.

Skeletons 5 (355-422). Western Australia (1); New South Wales (4).

Gymnosarda unicolor. Total 38 specimens (71.6-1,080 mm FL).

Dissected 6 (522-787). Amirante Islands (2); Truk Islands, Caroline Islands (3); Bikini, Marshall Islands (1, partial).

Measured and counted 31 (71.6-1,040). Red Sea (5, including holotype of *Thynnus unicolor* Rüppell); Comoro Islands (1); Amirante Islands (2); Madagascar (1); New Britain (1); Solomon Islands (2); Gilbert Islands (1); Japan (3); Palau Islands (1); Caroline Islands (7); Marshall Islands (5); Society Islands (1); Marquesas Islands (1).

Examined 1 (267-mm head of 1,080-mm specimen). Pitcairn Group.

Skeletons 11 (about 625-1,013). Amirante Islands (2); Marshall Islands (4); Truk Islands (3); unknown locality (2).

Orcynopsis unicolor. Total 55 specimens (164-960 mm FL).

Dissected 11 (332-645). Israel (5, partial); Tunisia (6, complete).

Measured and counted 43 (164-960). Lebanon (12, 242-325); Israel (12, 285-735); Egypt (5, 164-280); Tunisia (7, 312-645); Nice (1, 553); Mauritania (2, 400-410); Senegal (2, 405-960); Norway (2, 565-570, types of *Thynnus peregrinus* Collett).

Counts only 12 (417-950). Pizza (1, ca. 950); Elba (1, ca. 790); Gulf of Genoa (1, 670); Rimini, Adriatic (1, ca. 600); Egypt (6, 417-556); locality unknown (2).

Skeletons 11 (332-645). Israel (5); Tunisia (6).

Sarda australis. Total 21 specimens (195-495 mm FL).

Dissected 3 (360-495). New South Wales, Australia.

Measured and counted 21 (195-495). Norfolk Island (1); New South Wales (20, including holotype of *Pelamys australis* Macleay).

Skeletons 3 (360-495). New South Wales.

Sarda chiliensis–northeast Pacific. Total 91 specimens (207-643 mm FL).

Dissected 4 (401-472). La Jolla, Calif.

Measured and counted 24 (207-587). California: La Jolla; San Diego (including holotype of *Pelamys lineolatus* Girard); Los Angeles; San Pedro; Santa Barbara; Oceanside. Baja California: Coronados Island; Natividad Island; Cedros Island; Blanca Bay.

Counts only 21 (220-625). Vancouver, British Columbia (1); Alaska (2); S. California (17); Revillagigedos Island (1).

Skeletons 50 (310-643). S. California (including holotype of *Sarda stockii* (David)).

Sarda chiliensis–southeast Pacific. Total 44 specimens (57.2-672 mm FL).

Dissected 7 (437-571). Callao, Peru.

Measured and counted 23 (94.1-672). Valparaiso, Chile (holotype of *Pelamys chiliensis* Cuvier). Arica Bay, Chile. Peru: Callao; Foca Island; San Lorenzo Island; Pachacamac Island; Guañape Island; San Gallán Island.

Counts only 9 (57.2-636). Peru: San Lorenzo Island; San Gallán Island; Foca Island; Callao.

Skeletons 18 (437-571). Callao, Peru.

Sarda orientalis–Indo-West and central Pacific. Total 31 specimens (150-645 mm FL).

Dissected 5 (341-500). Tokyo (3); Hawaii (2).

Measured and counted 27 (150-645). South Africa (2); Seychelles Islands (1); Red Sea (2); Cochin, India (1); Western Australia (paratype of *Sarda orientalis serventyi* Whitley); China (4); Japan (12, including types of *Pelamys orientalis* Temminck and Schlegel); Hawaii (4).

Counts only 3 (223-370). Muscat (2); Ceylon (1).

Skeletons 6 (341-500). Muscat (1); Tokyo (3); Hawaii (2).

Sarda orientalis–eastern Pacific. Total 21 specimens (354-447 mm FL).

Dissected 4 (354-447). Navidad Bay, Mexico (1); Piñas Bay, Panama (2); Pearl Islands, Panama (1).

Measured and counted 12 (354-447). Mexico (1); Panama (8, including holotype of *Sarda velox* Meek and Hildebrand); Galapagos Islands (2); Gulf of Guayaquil (1).

Counts only 7 (429-650). Cabo San Lucas and Las Tres Marias Islands, Mexico (4); Galapagos Islands (3).

Skeletons 6 (354-447). Mexico (2); Panama (3); unknown locality (1).

Sarda sarda–western Atlantic. Total 86 specimens (118-637 mm FL).

Dissected 2 (333). New Jersey (1); Miami, Fla. (1).

Measured 29 (228-637). North America 12 (257-637): Massachusetts (4); New York (3); Chesapeake Bay (2); Florida (1); Cuba (1). Gulf of Mexico 5 (228-321): Florida (1); Texas (4). South America 12 (202-450): Gulf of Carioca, Venezuela (6); Brazil (5); Mar del Plata (1).

Counts only 51 (118-572). North America 39 (118-572): Massachusetts (24); Rhode Island (3); New York (3); New Jersey (1); Chesapeake Bay (2); Maryland (3); Florida (1). Gulf of Mexico 11 (103-400): Florida (3); Mississippi delta (3); Texas (1). South America 5 (214-570): Venezuela (1); Brazil (3); Mar del Plata (1).

Skeletons 9 (333-577). Massachusetts (2); Connecticut (1); New York (1); New Jersey (1); Florida (1); exact locality unknown (3).

Sarda sarda–eastern Atlantic. Total 62 specimens (104-680 mm FL).

Dissected 5 (363-504). Azores (3); Tunisia (1); Gulf of Guinea (1).

Measured and counted 30 (260-600). Atlantic Europe 9 (418-600): Norway (5); Spain (1); Azores (3). Mediterranean 8 (260-564). Black Sea 1 (550). Gulf of Guinea 10 (305-478). Port Elizabeth, South Africa 2 (447-517).

Counts only 31 (104-680). Europe 2 (482-670). Mediterranean 18 (187-487). Black Sea 9 (104-680). Gulf of Guinea 2 (366-375).

Skeletons 6 (363-504). Azores (3), Tunisia (1); Gulf of Guinea (2).

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KEY TO THE SPECIES OF SARDINI

1a. Jaw teeth tiny, 40-55 on each side of upper and lower jaws; gill rakers fine and numerous, total of 70-80 on first arch; body elongate, snout to second dorsal 610-654 thousandths of fork length; maxilla short, 354-379 thousandths of head length ..... *Allothunnus fallai* Serventy

1b. Jaw teeth larger and more prominent, 10-30 on each side of upper and lower jaws; total gill rakers on first arch 8-27; body less elongate, snout to second dorsal 481-610 thousandths of fork length; maxilla longer, 431-557 thousandths of head length 2

2a. Five to ten narrow, dark, longitudinal stripes on upper part of body; no teeth on the tongue; spleen prominent in posterior third of body cavity in ventral view ..... *Sarda* 3

2b. Body either without stripes or with dark spots above the lateral line and longitudinal dark stripes below; two patches of teeth present on tongue; spleen either concealed or located in anterior third of body cavity in ventral view 6

3a. Spines in first dorsal fin 20-23; total vertebrae 50-55 ..... *S. sarda* (Bloch)

3b. Spines in first dorsal fin 17-19; total vertebrae 43-46 4

4a. Total gill rakers on first arch 8-13; supramaxilla narrow (see Figure 32e) ..... *S. orientalis* (Temminck and Schlegel)

4b. Total gill rakers on first arch 19-27; supramaxilla wider (see Figure 32c-d) 5

5a. Total gill rakers on first arch 19-21; pectoral rays 25-27, modally 26; teeth sometimes present on vomer; length of first dorsal base 315-343 thousandths of fork length; maxilla 503-539 thousandths of head length ..... *S. australis* (Macleay)

5b. Total gill rakers on first arch 23-27; pectoral rays 22-26, modally 24 or 25; teeth never present on vomer; length of first dorsal base 267-314 thousandths of fork length; maxilla 460-503 thousandths of head length ..... *S. chiliensis* (Cuvier)

6a. Body with dark spots above lateral line and dark longitudinal stripes below (see Figure 1a); spines in first dorsal fin 16-18 ..... *Cybiosarda elegans* (Whitley)

6b. Body without a prominent pattern of stripes or spots (see Figure 2); spines in first dorsal fin 12-15 .....

7a. Pectoral rays 21-23; small conical teeth in jaws; total gill rakers on first arch usually 14 or more; interpelvic process bifid; spleen not visible in ventral view; laminae in olfactory rosette 25-28; interorbital width 239-310 thousandths of head length ..... *Orcynopsis unicolor* (Geoffroy St. Hilaire)

7b. Pectoral rays 25-28; jaw teeth very large and conspicuous; total gill rakers on first arch usually 13 or fewer; interpelvic process single; spleen visible on right side of body cavity in ventral view; laminae in olfactory rosette 48-56; interorbital width 321-400 thousandths of head length ..... *Gymnosarda unicolor* (Rüppell)

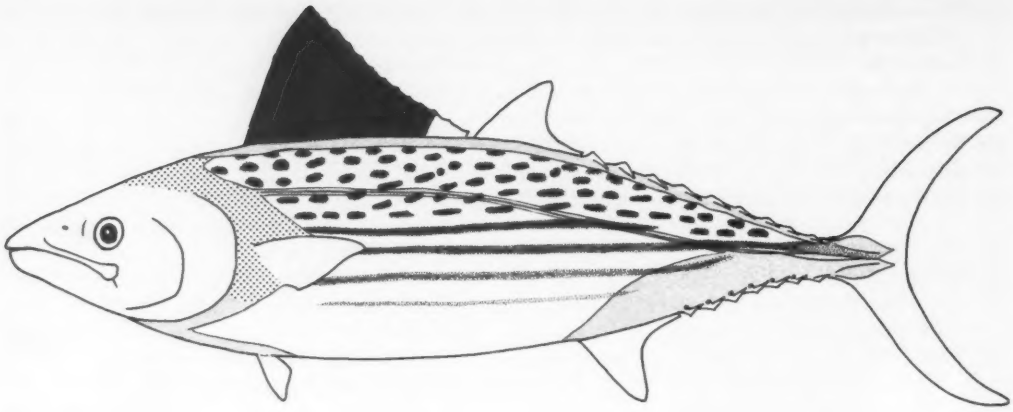
PART 1.
COMPARATIVE MORPHOLOGY

The morphological characters useful for distinguishing the species of bonitos and for evaluating their phylogenetic relationships are divided into six categories: color pattern, scales, morphometry, meristics, soft anatomy, and osteology.

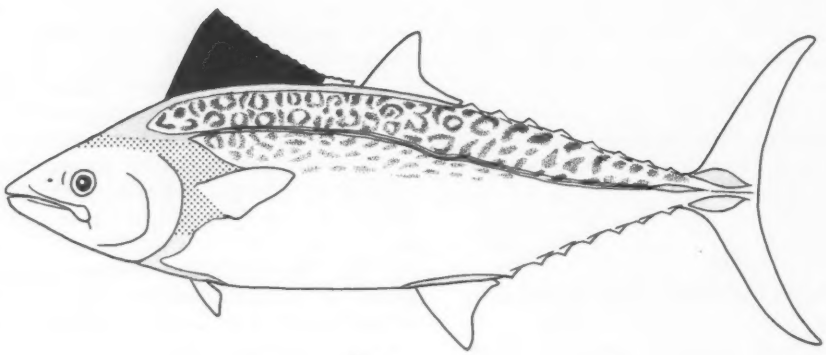
Color Pattern

The most strikingly colored species of the Sardini, and perhaps the entire family Scombridae, is clearly *Cybiosarda elegans* (Figure 1a). The light venter has several stripes reminiscent of the skipjack tuna, *Katsuwonus pelamis* (Linnaeus). The dorsum is covered with black spots over a deep blue background. The high first dorsal fin is jet black anteriorly and white posteriorly. The anal and second dorsal fins are yellow. *Orcynopsis unicolor* (Figure 1b) has a high black first dorsal fin as in *Cybiosarda*, but there the similarity ends because adult *Orcynopsis* have only a faint mottled pattern that has been deliberately exaggerated in the figure. All species of *Sarda* (Figure 1c) have stripes along their backs but the number of stripes and their alignment varies both interspecifically and intraspecifically. *Sarda australis* has stripes on the venter as well as on the dorsum. *Sarda* also has a black first dorsal fin but it is lower and longer than in *Cybiosarda* and *Orcynopsis*. *Gymnosarda unicolor* (Figure 2a) is deep blue without any distinct pattern; *Allothunnus fallai* (Figure 2b) also lacks distinctive markings.

Color plates have been published of all the species of bonitos except *Allothunnus*. Paintings of three Australian species by George Coates were published by Marshall (1964, 1966): *Cybiosarda elegans* (fig. 345), *Sarda australis* (fig. 348), and *Gymnosarda unicolor* (fig. 342). Color illustrations of *Orcynopsis unicolor* were published by Lozano y Rey (1952, pl. 41, fig. 2–800-mm adult and fig. 3–150-mm juvenile) and by Bini (1968:39). *Sarda sarda* was illustrated by La Monte (1945, pl. 8; 1952, pl. 17), Lozano y Rey (1952, pl. 39, fig. 4–500-mm adult), and Bini (1968:37). Walford (1937, pl.



a



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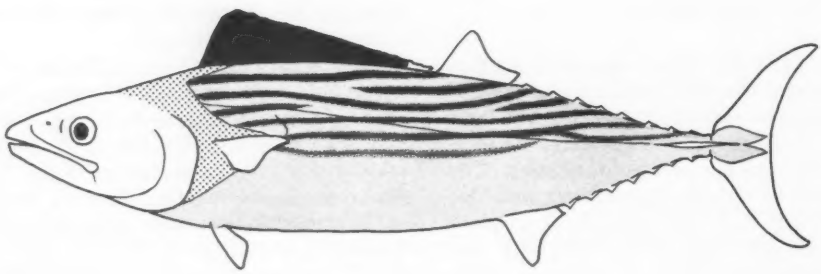


c

FIGURE 1.—Diagramatic lateral views of three species of Sardini to show general pigment pattern, extent of corselet (coarse stippling), and parts of the body covered by smaller scales (fine stippling). a. *Cybiosarda elegans*, New South Wales, 337 mm FL, USNM 259407-F2. b. *Orcynopsis unicolor*, Tunisia, 312 mm FL, USNM 206526. c. *Sarda sarda*, Gulf of Mexico, 287 mm FL, USNM 118646.

38) includes color photographs of a northeastern Pacific *Sarda chiliensis* and an eastern Pacific *S. orientalis*.

Scales

In bonitos, the body scales are cycloid and usually small. Those on the corselet, along the fin bases, and along the lateral line are larger and more elongate. The predorsal and opercular scales are larger and are embedded under the skin. No scales are present on the snout, the interorbital area, or on the fins. Posterior to the corselet, the distribution of scales differs among the genera of bonitos (Figures 1, 2). Species of *Sarda* have their body completely covered with small scales except for the distal portion of the caudal keels (Figure 1c). *Allothunnus* has the dorsal half of the body covered with scales (Figure 2b), but they do not extend onto the caudal keels, although they do cover the base of the caudal fin. Serventy (1948) described the type of *Allothunnus fallai* as having its whole body covered with scales. But later authors, Talbot (1960), Olsen (1962), and Nakamura and Mori (1966), all indicated that the minute scales of *Allothunnus* are present only on

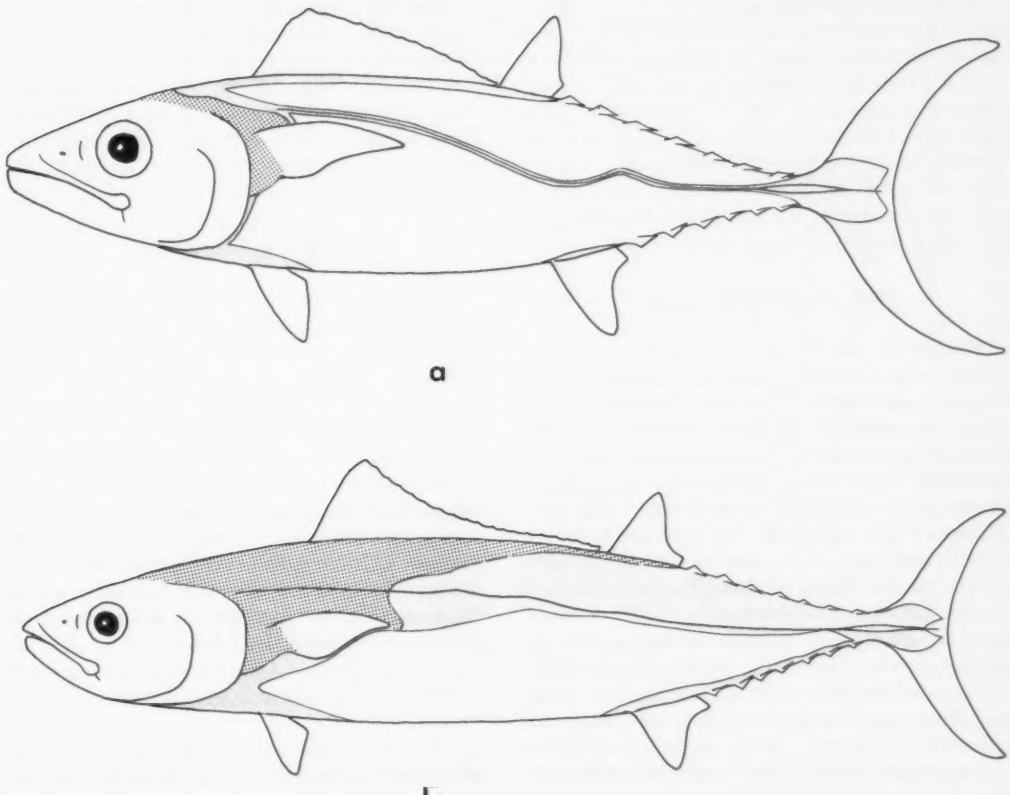


FIGURE 2.—Diagrammatic lateral views of two species of Sardini to show extent of corselet (coarse stippling) and parts of body covered by smaller scales (fine stippling). a. *Gymnosarda unicolor*, Tahiti, 446 mm FL, ANSP 93818. b. *Allothunnus fallai*, New Zealand, 642 mm FL.

the dorsal half of the fish. A patch of scales is also present around the base of the pelvic fins. *Cybiosarda* has a band of scales dorsally extending along the entire midline (Figure 1a). Ventrally, scales are present around the base of the pelvic fins and a broad band of scales extends from the anal fin origin posterodorsally to the caudal peduncle. The peduncular region is entirely covered with scales except for the distal margin of the caudal keel. *Orcynopsis* (Figure 1b) has fewer scales than *Cybiosarda*. The band of scales along the dorsal midline is narrower and ends at the dorsal finlets. Ventrally, *Orcynopsis* has scales around the bases of the pelvic and anal fins. The caudal peduncle is naked except for the caudal keel. *Gymnosarda* is completely naked posterior to the corselet except for the lateral line, dorsal fin base, and caudal keel (Figure 2a).

The corselet, composed of enlarged scales, is well defined in the pectoral region of bonitos. It extends from the dorsal end of the gill slit to the tip of the pectoral fin, except in *Sarda* and *Allothunnus*. Anterior and ventral to the pectoral fin base, the scales are smaller than on other parts of the corselet in bonitos. In *Sarda*, an extra wing of the corselet extends dorsally toward the origin of the first dorsal fin. *Allothunnus* has the most extensive corselet, covering most of the area between the first dorsal fin base and the pectoral fin.

Morphometric Characters

Twenty-six measurements, in addition to fork length, were routinely made on all specimens destined to be dissected to insure that these data would be available if needed. Preserved material was also measured until an adequate sample was obtained. Measurements follow the methods of Marr and Schaefer (1949) as modified by Gibbs and Collette (1967). Morphometric characters can be used to separate genera, species, and populations within species. Tables showing the 26 characters as thousandths of fork length and 8 characters as thousandths of head length are presented in the systematic section of the paper. Most of the characters are best used at the species level; therefore, only a summary table of the means of proportions (Table 1) is presented in this section.

Orcynopsis is short-bodied and short-headed. It has shorter snout-anal and snout-second dorsal distances than do the other bonitos. *Cybiosarda* is also relatively short-bodied. *Allothunnus* is the most elongate of the bonitos and has the greatest distances between the snout and the origins of the anal and second dorsal fins. *Cybiosarda* and *Orcynopsis* both have high first dorsal, second dorsal, and anal fins compared to other bonitos. *Gymnosarda* has a differently shaped head than do other bonitos: the interorbital distance is much wider, the eyes are larger, the postorbital distance is shorter, and the distance between the origins of the pectoral and pelvic fins is much larger. In addition, *Allothunnus* has large eyes and a very short snout and maxilla.

Because of small sample size, restricted geographical distribution, or both, morphometric data were combined for each of four species: *Cybiosarda elegans*, *Sarda australis*, *Gymnosarda unicolor*, and *Allothunnus fallai*. Three populations of *Orcynopsis unicolor* are compared: Israel, Lebanon, and Tunisia. The southeast Pacific population of *Sarda chiliensis* (nominal *S. c. chiliensis*) is compared with the northeast Pacific population (*S. c. lineolata*). The population of *Sarda orientalis* in the eastern tropical Pacific (nominal *S. o. velox*) is compared with the only other sufficiently large sample, northwest Pacific. Three populations of *S. sarda* are compared: western Atlantic, Mediterranean Sea (including the Black Sea), and the Gulf of Guinea.

Meristic Characters

Countable structures are of special value systematically because they are relatively easy to record unambiguously and because they are easy to summarize in tabular fashion. Meristic characters that have proved valuable systematically in the Sardini include numbers of fin rays (first dorsal spines, second dorsal rays, dorsal finlets, anal rays, anal finlets, pectoral rays), gill rakers, teeth (especially on the upper and lower jaws), vertebrae, and laminae in the olfactory rosettes. Olfactory laminae are discussed as the last section under soft anatomy. The other meristic characters are discussed in the relevant osteological sections of the paper.

Soft Anatomy

The relative position, shape, and size of the various internal organs provide valuable diagnostic characters. Within the genus *Sarda*, these characters are useful at the species level. For purposes of discussion, the characters in the soft anatomy are divided into five sections: viscera, vas-

TABLE 1.–Morphometric comparison of species and populations of Sardini. Means as thousandths of fork length or head length.

Character	*Cybiosarda elegans*	*Orcynopsis unicolor* Israel	Lebanon	Tunisia	*Sarda australis*	*Sarda chiliensis* NE Pacific	SE Pacific	*Sarda orientalis* NW Pacific	E Pacific	*Sarda sarda* NW Atlantic	Mediterranean	Gulf of Guinea	*Gymnosarda unicolor*	*Allothunnus fallai*
Fork length														
Snout — A	652	577	587	578	674	665	654	694	678	668	660	657	629	676
Snout — 2D	531	499	511	481	586	566	569	606	582	582	579	578	557	628
Snout — 1D	273	247	253	246	263	269	279	286	288	270	266	298	285	306
Snout — P_2	299	273	284	270	296	295	303	303	310	296	288	275	285	284
Snout — P_1	267	238	247	229	267	266	275	281	290	269	263	265	264	269
P_1 — P_2	125	113	122	—	116	123	118	113	114	111	104	111	139	110
Head length	266	235	243	231	267	263	272	278	284	264	259	271	261	258
Max. body depth	227	246	255	240	231	210	210	234	213	214	205	217	224	223
Max. body width	133	124	123	130	141	131	134	146	144	135	131	—	151	164
P_1 length	138	138	135	142	121	116	—	115	127	115	116	130	160	129
P_2 length	82	63	61	64	85	78	84	76	86	79	82	83	103	78
P_2 insertion-vent	327	294	288	300	390	353	341	392	367	366	370	357	332	371
P_2 tip-vent	262	230	228	233	290	276	269	311	280	282	285	266	229	293
Base 1D	254	246	248	241	326	297	286	306	292	311	311	311	262	319
Height 2D	108	128	117	126	86	83	97	78	94	80	95	91	102	93
Base 2D	121	117	133	120	103	93	94	93	95	96	104	107	77	72
Height anal	107	126	118	125	81	74	92	73	89	77	79	85	99	90
Base anal	91	114	111	106	78	71	74	73	79	73	78	80	62	72
Caudal spread	251	261	270	213	259	246	258	214	236	222	247	253	304	226
Snout (fleshy)	98	89	94	91	96	94	95	96	101	94	93	96	107	75
Snout (bony)	82	76	80	83	81	78	81	86	86	82	78	82	98	65
Maxilla length	130	113	123	112	139	126	130	145	150	136	131	138	138	93
Post orbital	136	112	117	—	130	139	142	139	146	136	132	138	101	139
Orbit (fleshy)	29	28	31	31	39	31	31	42	37	35	31	34	51	45
Orbit (bony)	58	51	57	52	66	57	56	56	54	57	57	60	73	63
Interorbital width	73	68	66	72	66	63	70	71	71	64	62	63	92	—
Head length														
Snout (fleshy)	367	381	387	396	361	357	348	344	357	358	358	353	410	292
Snout (bony)	308	326	328	358	305	297	299	308	303	309	303	301	374	252
Maxilla length	489	483	505	483	518	481	477	522	528	514	505	509	527	361
Post orbital	511	478	484	—	492	526	523	503	512	516	511	506	381	545
Orbit (fleshy)	109	121	129	107	137	119	115	136	130	133	118	122	196	175
Orbit (bony)	218	218	236	211	246	218	205	220	226	217	220	220	279	244
Interorbital width	273	289	272	297	249	239	257	256	251	242	238	231	353	224

cular system, pharyngeal muscles, urogenital system, and olfactory organ.

VISCERA

Emphasis was placed on the appearance of the viscera in ventral view, after removal of an oval segment of the belly wall (Figure 3). Important papers on the viscera of bonitos include Kishinouye (1923 - *Sarda* and *Gymnosarda*), Godsil (1954, 1955 - *Sarda*), Postel (1954 - *Orcynopsis*), Blanc and Postel (1958 - *Gymnosarda*), Silas (1963 - *Gymnosarda*), and Nakamura and Mori (1966 - *Allothunnus*).

General Description.–The anterior end of the liver abuts against the transverse septum anteriorly in the body cavity. There are usually three lobes to the liver: the middle lobe is conspicuous in ventral view in all bonitos, whereas one or both lateral lobes are visible only in *Gymnosarda* and *Sarda*. No striations are present on the surface of the liver as they are in four species of *Thunnus* (see Gibbs and Collette 1967). Two efferent (venous) vessels lead directly from the anterior surface of the liver into the sinus venosus in all species. The short esophagus leads into the stomach. The intestine arises from the anterior end of the stomach which extends posteriorly as a blind sac. The caecal mass covers 22-81% of the anterior part of the body cavity and opens into the intestine immediately posterior to the junction of intestine and stomach. The intestine forms a loop anteriorly. The remainder of the digestive tract is straight in *Sarda*, but two additional loops are present in the mid-intestine of *Cybiosarda*, *Gymnosarda*, and *Orcynopsis*.

The spleen is prominent in ventral view in *Gymnosarda* and *Sarda*, but is hidden by the liver and caecal mass in *Allothunnus*, *Cybiosarda*, and

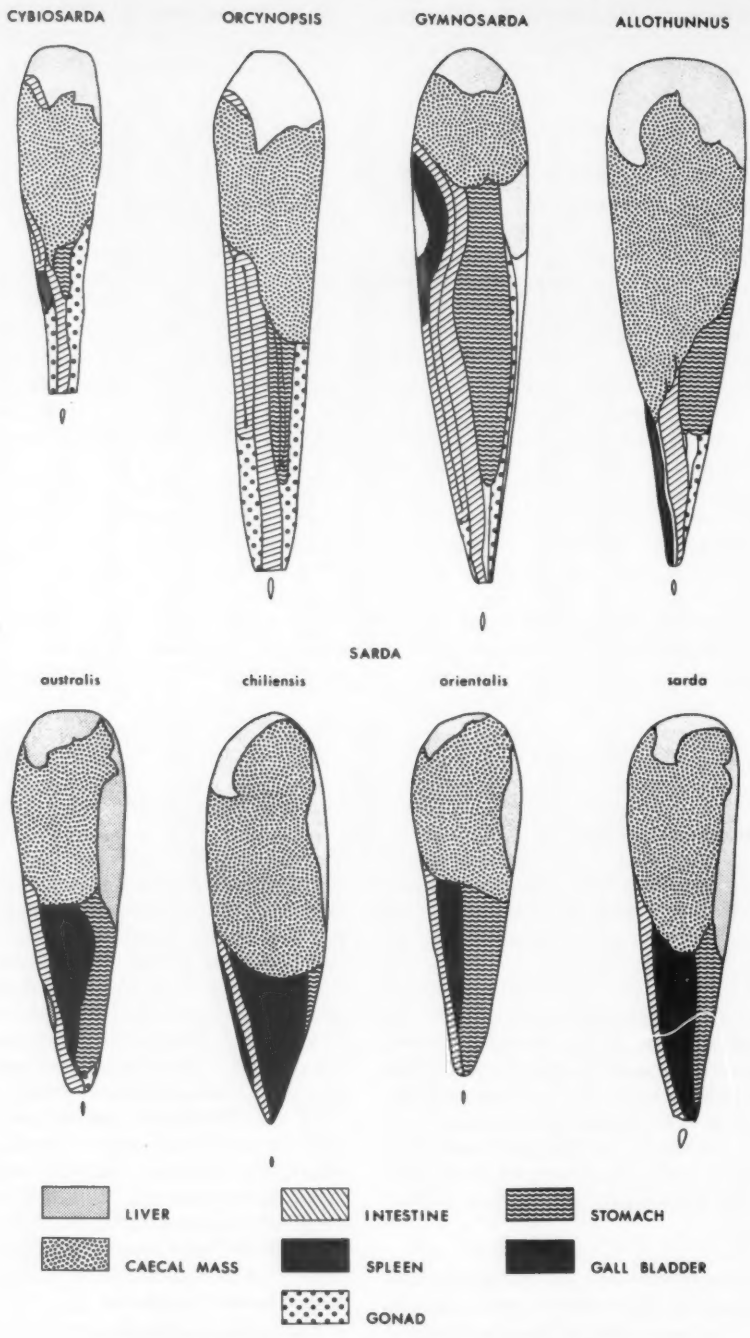


FIGURE 3.—Viscera, in ventral view, of the eight species of Sardini.

Orcynopsis. The gall bladder, an elongate tubular sac which is usually green in color, arises from the right lobe of the liver and usually lies along the intestine on the right hand side. The stomach extends further posteriorly and is more prominent in ventral view when it is full. The mature ovary is sometimes large enough to cover the stomach ventrally. A swim bladder is absent in all bonitos except *Gymnosarda*.

Specific Characters.—The bonitos are divided into three groups based on the shape of the liver (Figure 4). *Sarda* and *Gymnosarda* have three distinct liver lobes; both lateral lobes are elongate and much longer than the middle lobe; the right lateral lobe is always longer than the left lateral lobe. All three lobes in *Gymnosarda* are visible ventrally if the dissection extends far enough laterally. In addition, the connection of middle and left lobes is visible anteroventrally in *Sarda*. *Orcynopsis* and *Cybiosarda* have an elongate right lateral lobe and a very short left lateral lobe which tends to fuse with the middle lobe. *Allothunnus* differs from the other genera in having three subequal lobes, as in the bluefin tuna group of species of *Thunnus*.

The bonitos can be divided into three groups based on the relative length of the caecal mass. *Allothunnus* has the longest caecal mass (71-81% of body cavity length, $\bar{x}$ 76.4%) of any of the bonitos followed by *Cybiosarda* (65-72%, $\bar{x}$ 69.2%) and *Orcynopsis* (46-59%, $\bar{x}$ 56.3%). *Gymnosarda* has the shortest caecal mass (22-30%, $\bar{x}$ 25.2%). The species of *Sarda* are intermediate between these two groups, most having the caecal mass about half the length of the body cavity (*S. australis* 44-55%, $\bar{x}$ 49.7; *S. sarda* 38-58%, $\bar{x}$ 48.3; and *S. orientalis* 41-50%, $\bar{x}$ 46.7). There is significant geographic variation in the fourth species, *S. chiliensis*. Three northeast Pacific specimens have a distinctly longer caecal mass (61-65%, $\bar{x}$ 62.3) than six southeast Pacific specimens (40-53%, $\bar{x}$ 48.5). This

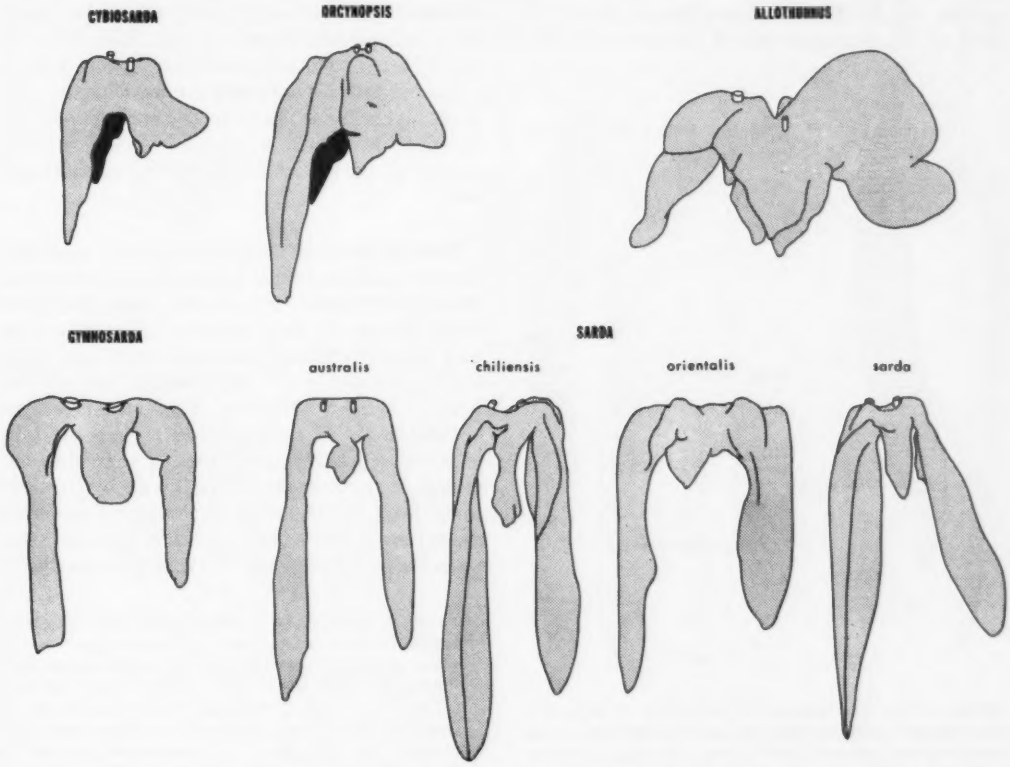


FIGURE 4.—Ventral view of excised livers of eight species of Sardini. Spleen shown in black for *Cybiosarda* and *Orcynopsis*.

tendency supports the findings of Godsil (1955). However, a seventh southeast Pacific specimen had a considerably longer caecal mass (70%) than our other six specimens.

The position and size of the spleen are distinctive among the genera. Species of *Sarda* have a large spleen, the major portion of which is located in the posterior half of the body cavity between the intestine and the stomach in ventral view. The spleen of *Gymnosarda* is also visible ventrally, but it is smaller than in *Sarda* and located in the anterior half of the body cavity. In *Orcynopsis* and *Cybiosarda*, the spleen is hidden by the right lobe of the liver and caecal mass. The spleen was visible in ventral view in one specimen of the four *Allothunnus* examined.

The number of loops in the intestine separates *Sarda* and *Allothunnus* from the other three genera of bonitos. In *Sarda* and *Allothunnus*, the intestine leaves the stomach and then moves posteriorly along the right side of the body cavity straight to the anus (Figure 5a). In the other genera, the intestine makes a loop at about the level of the posterior end of the stomach, runs anteriorly almost to where it came off the stomach, forms another loop, and then goes straight posteriorly to the anus (Figure 5b).

The caecal mass is connected to the anterior part of the intestine by 6-9 ducts as shown diagrammatically in Figure 5. Each of the main ducts branches into numerous smaller ducts within a short distance from the intestine. We did not count the number of ducts often enough to determine the systematic value of this character and so merely present the results for six specimens: *Cybiosarda*–3 anterior and 5 posterior ducts in one specimen, 3 anterior and 6 posterior in another; *Sarda australis*–3 anterior and 4 posterior; *S. chiliensis*–2 anterior and 4 posterior; *S. orientalis*–3 anterior and 4 posterior; and *Gymnosarda*–a total of 6 ducts.

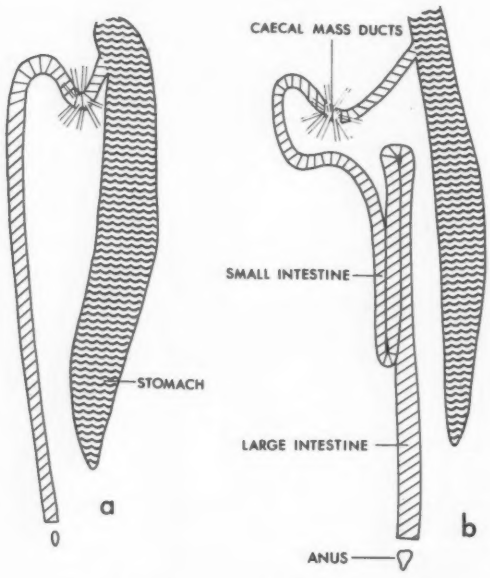


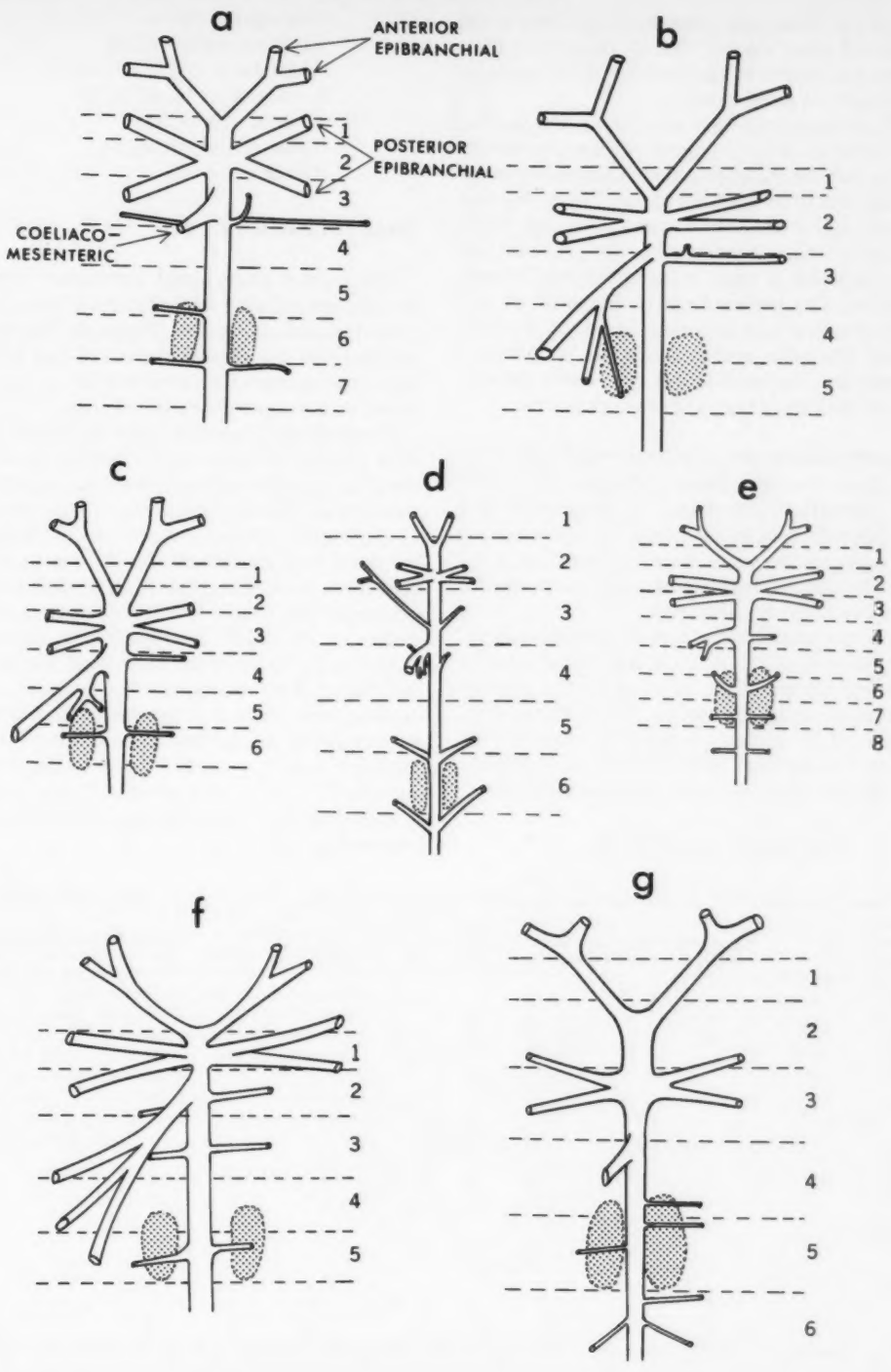
FIGURE 5.–Course of intestine from stomach, through area where the ducts of the caecal mass empty into the intestine, to the anus in two species of Sardini, ventral view (diagrammatic). a. *Sarda orientalis*, Tokyo, 341 mm FL. b. *Cybiosarda elegans*, New South Wales, 365 mm FL.

VASCULAR SYSTEM

The only published work on the vascular system of the bonitos is on the Pacific species *Sarda orientalis* by Kishinouye (1923) and Godsil (1954, 1955) and on *S. chiliensis* by Godsil (1954, 1955). No specialized subcutaneous vascular system and no cutaneous arteries or veins are present as they are in the higher tunas, *Auxis* to *Thunnus*. Therefore, this description will be confined to the anterior portion of the dorsal aorta and the postcardinal vein.

General Description.–The efferent branchial (epibranchial) arteries and coeliaco-mesenteric artery form a unit at the anterior end of the dorsal aorta (Figure 6). Two anterior epibranchials on each side unite to form a common trunk, and these trunks join as the "Y" of the aorta beneath the first or second vertebra. The posterior two epibranchials of each side unite immediately before they join the aorta, usually ventral to the second or third vertebra. As the aorta proceeds posteriorly it gives rise to the large coeliaco-mesenteric artery on the right side ventral to the second to fourth vertebra. The coeliaco-mesenteric

FIGURE 6.–Anterior part of arterial system in seven species of Sardini. Numbers indicate vertebral centra; stippled areas show where pharyngeal muscles originate. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 543 mm FL. c. *Sarda australis*, New South Wales, 408 mm FL. d. *Sarda orientalis*, Tokyo, 500 mm FL. e. *Sarda sarda*, eastern United States, 388 mm FL. f. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. g. *Allothunnus fallai*, Tasmania, 764 mm FL.


a
ANTERIOR EPIBRANCHIAL
POSTERIOR EPIBRANCHIAL
COELIACO-MESENTERIC
1
2
3
4
5
6
7
b
1
2
3
4
5
c
1
2
3
4
5
6
d
1
2
3
4
5
6
e
1
2
3
4
5
6
7
8
f
1
2
3
4
5
g
1
2
3
4
5
6

has two or three main branches which lead to the liver and other viscera. Godsil (1954, 1955) illustrated and described the branches of the coeliaco-mesenteric in great detail.

The postcardinal vein runs along the ventral surface of the kidney (Figure 7) from the vicinity of the first complete haemal arch anteriorly in the median line to the pectoral region. There it curves to the right and discharges into the right Cuvierian duct. Posteriorly, the postcardinal receives a pair of small veins at the level of each vertebra. The postcardinal is composed of two main branches that join anterior to the Y of the ureter. The main branch leaves the haemal arch dorsally and the small branch runs under the surface of the kidney from the urogenital area.

Specific Characters.—Variation was found in the location of the components of the anterior part of the arterial system (Table 2). *Orcynopsis* and *Gymnosarda* tend to have both the epibranchials and coeliaco-mesenteric more anterior than in the other bonitos (ventral to first vertebra vs. second, second vs. third, respectively).

To locate which haemal arch the dorsal branch of the postcardinal enters, a pin was forced into the vertebral column at the point where the postcardinal came up to the surface of the kidney. The number of the vertebra bearing this haemal arch was then determined at the end of the dissection. The number of the vertebra varied as follows:

Cybiosarda 15, 16, 17, 17
Orcynopsis 16
Sarda australis 17, 18
S. chiliensis 16, 17, 17, 19, 21
S. orientalis 15, 16, 18, 19
S. sarda 18, 19, 20
Gymnosarda 16, 16, 17
Allothunnus 21

PHARYNGEAL MUSCLES

The paired pharyngeal (retractor dorsalis) muscles are included on the figures of the anterior part of the arterial system (Figure 6). The muscles originate on the ventral surface of one to three vertebrae between the fourth and the seventh and insert on the upper pharyngeal bones.

The pharyngeal muscles insert on the fourth and fifth vertebra in *Gymnosarda* and are mostly on the fifth or sixth vertebra in the other bonitos. The data are as follows: *Cybiosarda* 6 (3 specimens), 5 (1 specimen), 7 (1 specimen); *Orcynopsis* 5 extending onto 4 (4 specimens); *Sarda australis* 6 (3 specimens, extending onto 7 in 1 specimen); *S. chiliensis* NE Pacific 6 and 7 (2 specimens); *S. chiliensis* SE Pacific 5 (5 specimens, extending onto 6 in 3); *S. orientalis* Indo-West Pacific 6 (2 specimens), 5 extending onto 4 (1 specimen), 6 extending onto 7 and 5 (1 specimen); *S. orientalis* eastern Pacific 6 (4 specimens, extending onto 7 in all 4, onto 5 in 1); *S. sarda* 6 (3 specimens, extending onto 7 in 2 specimens, onto 5 in 1); *Gymnosarda* 4 extending onto 5 (3 specimens); and *Allothunnus* 5 extending onto 4 (1 specimen).

TABLE 2.—Location of "Y" of aorta, posterior epibranchials, and the coeliaco-mesenteric artery, in the eight species of Sardini.

Structure under vertebra no.	*Cybiosarda elegans*	*Orcynopsis unicolor*	*Sarda australis*	*Sarda chiliensis* SE Pac.	*Sarda chiliensis* NE Pac.	*Sarda orientalis* Indo-W Pac.	*Sarda orientalis* E Pac.	*Sarda sarda*	*Gymnosarda unicolor*	*Allothunnus fallai*
Y of aorta										
skull									1	
skull-1	3	1		2					2	
1	2	5	1	1	1	2	1	2	1	1
1-2		2	—	2	2	—	2	1	—	1
2			2			3	1	2	1	2
2-3										
Posterior epibranchials										
1		2		1					2	
1-2		3		1					2	
2	3	2		2	2	3	2	2	1	
2-3	1		1	1		1	1	1		2
3	1		2			1	1	1		1
Coeliaco-mesenteric										
1-2		1								
2		1							3	
2-3		3		1					1	
3	2	3		2	3	2	1		1	1
3-4	2		1	—		1	1	1		1
4	1		2	2		2	2	3		1

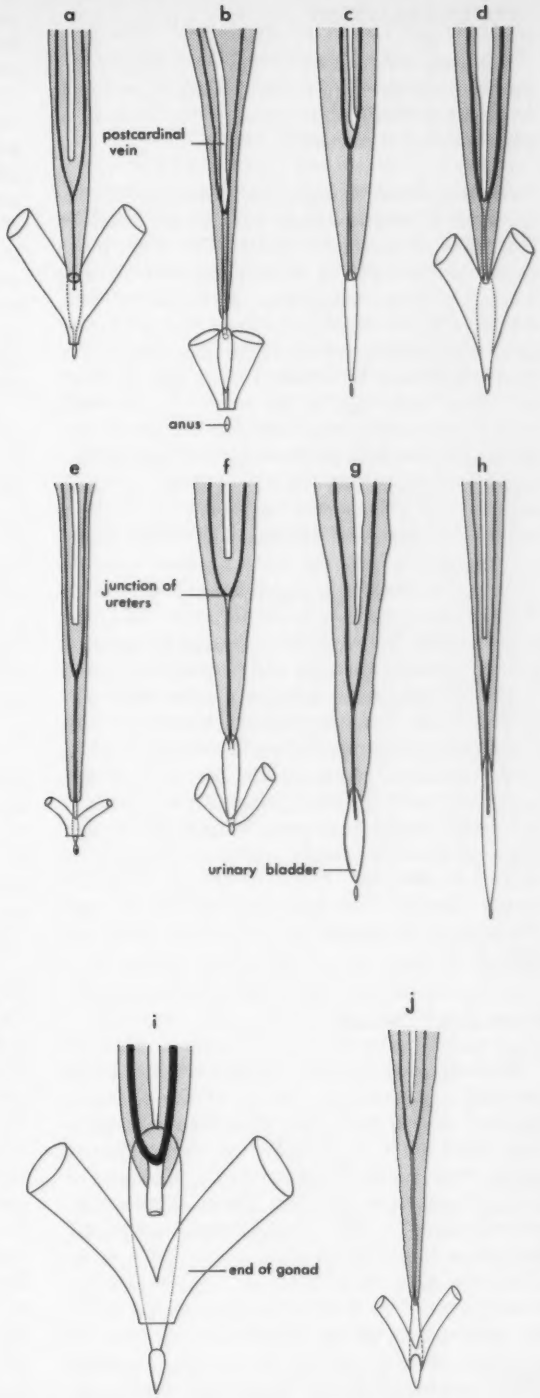


FIGURE 7.–Ventral view of posterior part of kidney showing postcardinal vein, junction of ureters, and urinary bladder in eight species of Sardini. Posterior ends of gonads shown in some figures. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Cybiosarda elegans*, New South Wales, 360 mm FL. c. *Orcynopsis unicolor*, Tunisia, 567 mm FL. d. *Orcynopsis unicolor*, Tunisia, 593 mm FL. e. *Sarda australis*, New South Wales, 355 mm FL. f. *Sarda chiliensis*, La Jolla, Calif., 472 mm FL. g. *Sarda orientalis*, Tokyo, 500 mm FL. h. *Sarda sarda*, Tunisia, 504 mm FL. i. *Gymnosarda unicolor*, Truk Islands, 787 mm FL. j. *Allothunnus fallai*, Tasmania, 764 mm FL.

UROGENITAL SYSTEM

The only references to the anatomy of the urogenital system are those of Kishinouye (1923) on *Sarda orientalis* and Godsil (1954, 1955) on *S. orientalis* and *S. chiliensis*.

General Description.—The paired gonads lie along the dorsolateral body wall and are visible in ventral view in mature adults. The kidney lies dorsal to the layer of fibrous connective tissue which forms the dorsal layer of the peritoneum. Anteriorly, the kidney divides into a pair of narrow projections which extend along the sides of the parasphenoid and usually reach the posterior end of the "mid-ridge" of the prootic. The anterior ends of the kidney surround the origins of the pharyngeal muscles on the vertebral column and usually separate along the middle of the vertebral column. The kidney may be absent in the area between the vertebrae and where the epibranchial arteries join to form the aorta. In some cases in each species, the kidney is well developed dorsal to this area and even covers the posterior end of the parasphenoid. In the vicinity of the esophagus, the kidney expands laterally and forms two projections which may reach anteriorly to the upper end of the gill slits. Posteriorly, near the posterior fifth of the body cavity, the kidney narrows to an elongate triangle (Figure 7). The branches of the ureter join to form a common trunk which leads to the urinary bladder between the gonads. The distance between the junction of the ureters and the urinary bladder and the size of ureters varies intraspecifically. The urinary bladders appear similar in all the bonitos, but no detailed study was made of them.

OLFACTORY ORGAN

General Description.—Kishinouye (1923) provided a generalized account of the olfactory organ of several scombrids. More detailed studies have been made on *Scomber scombrus* (Burne 1909), *Sarda sarda* (Tretiakov 1939), *Allothunnus fallai* (Nakamura and Mori 1966), *Katsuwonus pelamis* (Gooding 1963), and *Thunnus* (Iwai and Nakamura 1964b; Gibbs and Collette 1967). As in other scombrids, the olfactory cavity in bonitos has a small anterior naris and a slitlike posterior naris. No information on the supplementary sacs, or accessary olfactory cavity (Iwai and Nakamura 1964b), was obtained from the present study comparable to that of Tretiakov (1939), who described three supplementary sacs (middle, maxillary, and rostral sacs) in *S. sarda*. The central axis of the olfactory rosette is located beneath the anterior naris. Leaflike laminae radiate from the central axis and occupy the anterior dorsal third of the olfactory cavity. Gooding (1963) studied the morphology and histology of the olfactory organ of *Katsuwonus pelamis* and found olfactory cells on the olfactory epithelium of the laminae. Iwai and Nakamura (1964b) were the first to use the number of laminae to distinguish species of scombrids, but Gibbs and Collette (1967:91) felt additional material was necessary to validate the character in *Thunnus*.

We counted the number of olfactory laminae (by averaging both sides and rounding upward) in bonitos and found a rather wide range of variation (Table 3). Gooding (1963) also found a wide variation in *Katsuwonus*: 38-47 laminae per rosette in 38 skipjack olfactory rosettes. The number of laminae increases from small specimens to adults but does not appear to change after a certain size is reached. For example, 15 specimens of *Orcynopsis unicolor* (242-645 mm FL) had 25-28 laminae, a 178-mm specimen had 22, and a 164-mm specimen had 23. Twelve *Gymnosarda unicolor* (400-940 mm FL) had 48-56 laminae; a 306-mm specimen, 45; a 215-mm specimen, 43; and a 71.6-mm specimen, 27. Looking only at adults and subadults (Table 3), *Gymnosarda* has the highest number of olfactory laminae (48-56) and is completely separated from the other bonitos (21-39) in this character. *Orcynopsis*, *Cybiosarda*, and *Sarda australis* form a series with increasing numbers of laminae.

The pigmentation of the olfactory rosette varied in preserved specimens. In *S. australis* and *Orcynopsis* the dorsal margins of the olfactory laminae were pigmented and gave a radial pigmentation to the olfactory rosette. Black spots were found on the laminae of a specimen of *Cybiosarda* (Figure 8a). The fleshy ring of *S. sarda* showed grayish pigmentation in large specimens. No specific pigmentation was noted in other species of bonitos. The morphology of each olfactory lamina (Figure 8) is similar in each olfactory rosette, but decreased in size anteriorly. The olfactory cavity and accessary cavity are similar in all bonitos, except in *Cybiosarda* where the opening of the accessary sac was more dorsally located and led interiorly rather than interior-ventrally as in other bonitos.

TABLE 3.–Number of laminae in olfactory rosettes in species of Sardini. (Means based on original data not combined frequency distribution.)

Species	20-1	22-3	24-5	26-7	28-9	30-1	32-3	34-5	36-7	38-9	40-1	42-3	44-5	46-7	48-9	50-1	52-3	54-5	56-7	*N*	$\bar{x}$
Orcynopsis unicolor			2	8	5															15	26.9
Cybiosarda elegans					1	5	3													9	30.8
Sarda australis								1	1	4										6	37.2
S. chiliensis:																					
NE Pacific	1	2	8	7	1	1														20	25.4
SE Pacific		3	4	6	2															15	25.5
S. orientalis:																					
Red Sea - Indian Ocean			2	—	—	2	2	4												10	31.4
NW Pacific			2	—	1	1	1													5	28.0
Cent. Pacific			1	—	—	1	—	—	1											3	30.7
E Pacific						1	4	3	4											12	34.3
S. sarda:																					
North America		1	3	2	3	2	4													15	27.5
South America					2															2	28.5
Mediterranean - Black Sea		2	5	—	—	2														9	25.1
Gulf of Guinea - South Africa		1	3	1	2															7	25.4
Gymnosarda unicolor															4	1	3	3	1	12	51.6
Allothunnus fallai					2	1														3	29.0

Specific Characters.–A fleshy ring (Iwai and Nakamura 1964b) was found along the posterior margin of the olfactory rosettes in some bonitos. This fleshy ring is the continuation of the well-developed distal end of the olfactory laminae and forms a fleshy elevated area in species of *Sarda*. In *S. sarda* the fleshy ring usually develops in larger specimens (over 360 mm FL) as a folded fleshy pad (Figure 8h). Different developmental stages of the fleshy pad were found in all species of *Sarda* except in *S. c. chiliensis* which had no apparent rings. No fleshy ring or pad was found in *Cybiosarda* or *Orcynopsis* (Figure 8a, b). In *Gymnosarda*, a very definite fleshy ring surrounds all the olfactory laminae (Figure 8i) except in a juvenile specimen (71 mm FL), which had an elongated oval rosette with only 27 laminae. Nakamura and Mori (1966) found the olfactory rosette of *Allothunnus* to have labial fleshy rings around the olfactory laminae, similar to our observations (Figure 8j).

Osteology

Osteological characters proved to be very useful in determining how many genera of Sardini should be recognized. The osteological description is divided into five sections: skull, axial skeleton, dorsal and anal fins, pectoral girdle, and pelvic girdle. Osteological terminology generally follows de Sylva (1955) and Gibbs and Collette (1967) with a few changes to bring this nomenclature into closer agreement with more modern terminology.

SKULL

Description of the skull is presented in two sections: neurocranium and branchiocranium. Figure 9 shows an articulated skull of *Gymnosarda unicolor* in lateral view to provide orientation for the descriptions of the individual bones.

Neurocranium

Following a general description of the neurocranium, the four major regions are discussed: ethmoid, orbital, otic, and basicranial. Descriptions of the otoliths are included at the end of this section.

General Characteristics.–In dorsal view, the neurocranium of bonitos is roughly triangular in shape. The interorbital and otic regions are not as

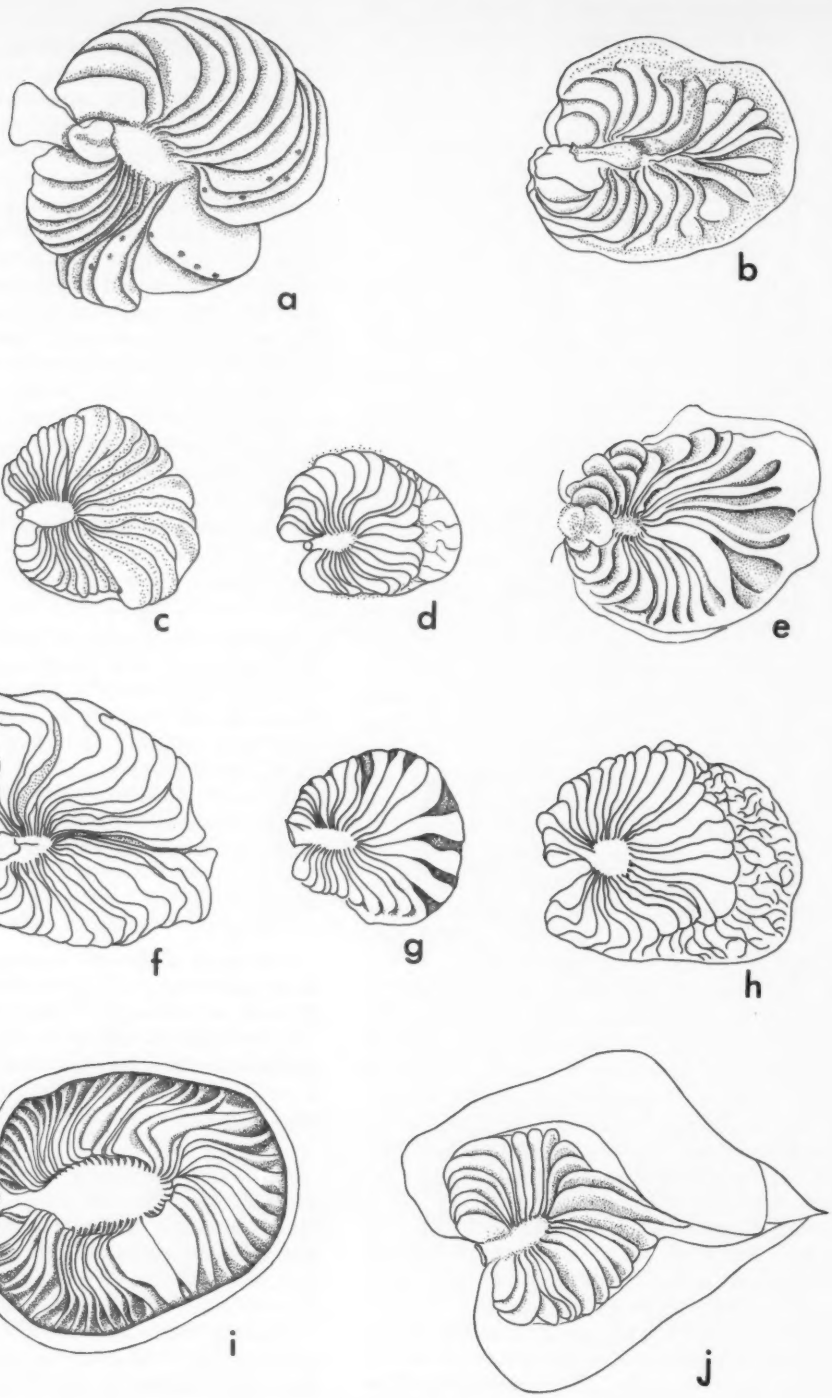

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FIGURE 8.–Olfactory rosettes (left) of eight species of Sardini. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, USNM 59881, 332 mm FL. d. *Sarda chiliensis*, Santa Barbara, Calif., USNM 31104, 335 mm FL. e. *Sarda chiliensis*, Callao, Peru, 571 mm FL. f. *Sarda orientalis*, Pearl Island, Panama, USNM 128644, 505 mm FL. g. *Sarda sarda*, Portuguese Guinea, 361 mm FL. h. *Sarda sarda*, Chesapeake Bay, 436 mm FL. i. *Gymnosarda unicolor*, Bikini, USNM 140980. j. *Allothunnus fallai*, New Zealand, DM 2472, 740 mm FL.

broad as in the most advanced scombrid genera–*Thunnus*, *Euthynnus*, *Katsuwonus*, and *Auxis* (Kishinouye 1923; de Sylva 1955; Gibbs and Collette 1967), but are broader than in the more primitive genera–*Scomber*, *Rastrelliger*, *Grammatorcynus*, *Scomberomorus*, and *Acanthocybium* (Allis 1903; Kishinouye 1923; Conrad 1938; Mago Leccia 1958; Gnanamuttu 1971), except in *Gymnosarda* which has a broad and short skull (Figure 10; Kishinouye 1923, fig. 38). *Allothunnus* has a more elongate and narrow skull (Figure 11) than do other bonitos. Bonitos lack the prominent frontoparietal foramen (Gibbs and Collette 1967) which is present on each side of the dorsal surface of the skull at (or near) the junction of the frontal, parietal, and supraoccipital bones of the three most advanced genera of Scombridae: *Euthynnus*, *Katsuwonus*, and *Thunnus*. The corresponding junction in bonitos does have a small hole and/or an area of very thin dermal bone (see Figure 12 of *Sarda sarda*). Two prominent dorsolateral crests are present on each side of the neurocranium (Figures 10-14). The inner crest arises at the anterolateral edge of the frontal bone, extends along the frontal and parietal bones, and terminates at the posterolateral corner of the epiotic bone. This crest is a thin bony process in all bonitos except *Allothunnus*, in which it arises from the posterior half of the frontal bones and has a much thicker and wider anterior half than do the other scombrid genera mentioned above. The primitive scombrid *Grammatorcynus* resembles *Allothunnus* in this character. The outer crest (Figure 11), which constitutes the posterolateral margins of the neurocranial roof, is formed by the edges of the frontal and pterotic bones. It originates at the posterolateral region of the frontal bones and extends posteriorly as a flat pterotic spine. The

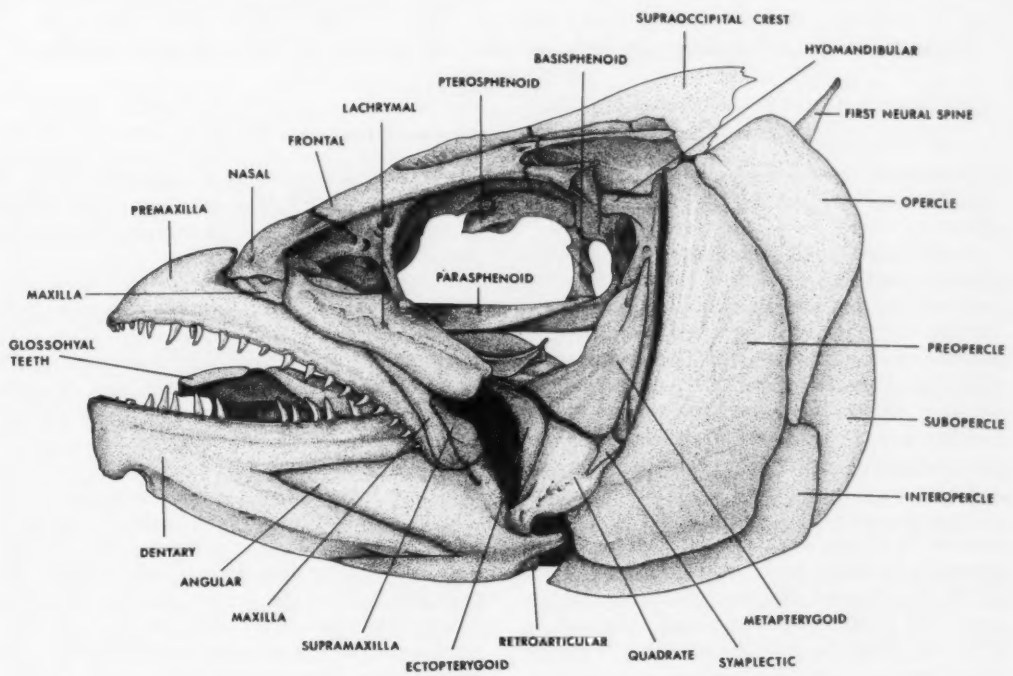


FIGURE 9.–Lateral view of head of *Gymnosarda unicolor*, Bikini, Marshall Islands, USNM 11478, 750 mm FL.

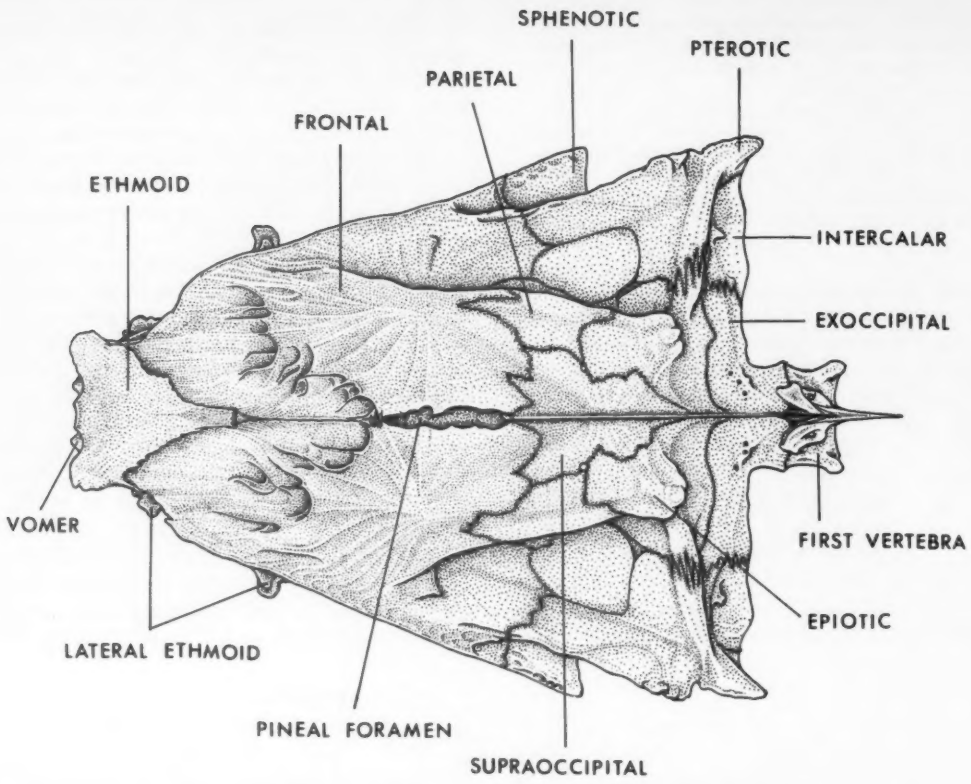


FIGURE 10.—Dorsal view of skull of *Gymnosarda unicolor*, Truk Islands, 696 mm FL.

supraoccipital crest is high and usually does not extend posteriorly past the tip of the first neural spine.

A prominent pineal foramen (Figures 10-14) is present anterior to the supraoccipital crest between the median edges of the frontal bones. Among the bonitos, it is most prominent in *Allothunnus*. Other scombrids either have a reduction in the thickness of the bone in this area (*Scomber*, *Rastrelliger*, and *Scomberomorus*) or a similar pineal foramen (*Grammatorcynus*, *Acanthocybium*, *Auxis*, *Euthynnus*, *Katsuwonus*, and *Thunnus*). In life, the pineal foramen is filled with a translucent cartilaginous lens and is covered by a layer of skin usually having an unpigmented window dorsal to the cartilage. Rivas (1953) hypothesized that, by permitting light to reach the pineal body, the pineal apparatus in *Thunnus* could be instrumental in controlling phototactic movements involved in migration. Holmgren (1958) concluded that while there are morphological indications of light sensitivity in the pineal area of *T. thynnus*, there is not enough physiological evidence to be sure of possible hormonal control by this area.

Ventrally (Figures 15-19), the prelateral ethmoid region of bonitos is shorter and broader than in other scombrids. The ventral surface of the skull is formed by the vomer, lateral ethmoids, and parasphenoid and is broader than that of more advanced scombrids. The anterior three-fifths of the parasphenoid is almost flat, there is a medial, ventral keel in the next fifth, and posteriorly it is thin and smoothly curved into lateral flanges which enclose a parasphenoidal chamber (Kishinouye 1923). The lateral wings of the parasphenoid project dorsolaterally from the posterior half of the ventral keel to form the anteroventral part of the posterior myodome. The ventral surface of the brain case is formed by the frontal, pterosphenoid, sphenotic, prootic, basioccipital, exoccipital, intercalar, and pterotic bones.

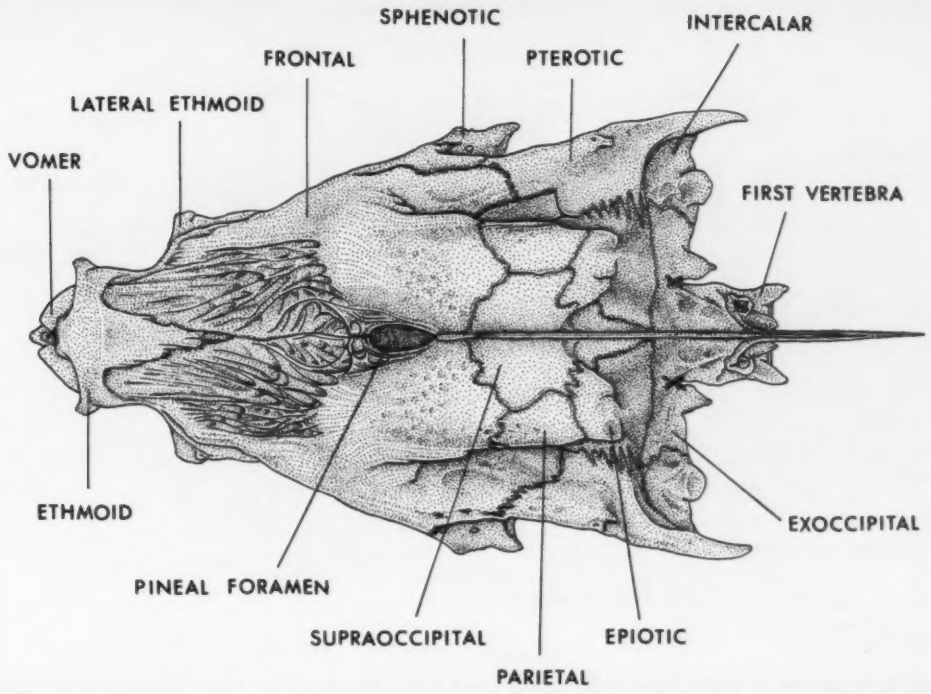


FIGURE 11.—Dorsal view of skull of *Allothunnus fallai*, California, 680 mm FL. X's indicate the points of attachment of intermuscular bones.

In lateral view (Figures 20-24), bonito skulls are similar to more advanced scombrids, but are more elongate and have the roof of the orbit less fully arched. *Allothunnus* (Figure 24) is most distinct in having a more pointed anterior end and a deeper posterior portion. The pterosphenoids project ventrally from the roof of the skull and form a partial interorbital septum which never fuses with the parasphenoid as in large *Thunnus thynnus* (see Gibbs and Collette 1967). In the posterior part of the orbit, the basisphenoid bisects the orbital capsule by connecting the pterosphenoids and prootic bones to the parasphenoid. The orbit is formed by the posterior edge of the lateral ethmoid, the ventral surface of the frontal and pterosphenoid, the parasphenoid, basisphenoid, and the anterior edge of the prootic. As expressed by the ratio of orbit height to length (see section on orbital region), the orbit is low and elongate in bonitos (Table 4); *Cybiosarda*, *Orcynopsis*, and *Sarda* have the lowest orbits as in *Scomberomorus* and *Acanthocybium*. *Gymnosarda* and *Allothunnus* each have a more highly arched orbit resembling that in *Scomber*, *Grammatorcynus*, *Rastrelliger*, *Auxis*, *Euthynnus*, *Katsuwonus*, and *Thunnus* (Allis 1903; Kishinouye 1923; Mago Leccia 1958; Gibbs and Collette 1967; Gnanamuttu 1971).

TABLE 4.—Ratio of orbit height to length in species of Sardini.

Species	Range	$\bar{X}$	*N*	Skull length (mm)	Fork length (mm)
Orcynopsis unicolor	3.85-4.60	4.32	6	43.2-71.2	323-620
Cybiosarda elegans	3.83-5.37	4.49	4	48.6-64.3	355-422
Sarda australis	3.03-3.70	3.33	3	23.1-29.6	363-495
Sarda chiliensis:					
SE Pacific	3.78-6.69	5.12	17	26.7-86.7	437-571
NE Pacific	3.10-5.78	4.12	37	24.3-92.3	332-570
Sarda orientalis:					
Indo-W Pacific	3.67-4.30	4.06	3	47.8-68.8	340-500
E Pacific	3.20-5.09	4.03	7	50.9-68.0	354-497
Sarda sarda	3.42-5.00	3.92	7	45.6-66.1	333-504
Gymnosarda unicolor	2.26-2.68	2.45	5	102-120	625-772
Allothunnus fallai	2.94-3.40	3.19	4	72.4-114	406-778

The posterior part of the base of the cranium is formed by the lateral flanges of the parasphenoid (ventral profile) and basioccipital (posterior profile). Along the dorsal profile, a crest formed anteriorly by the joint between the frontals is most distinctive in *Sarda*, as in *Scomberomorus*

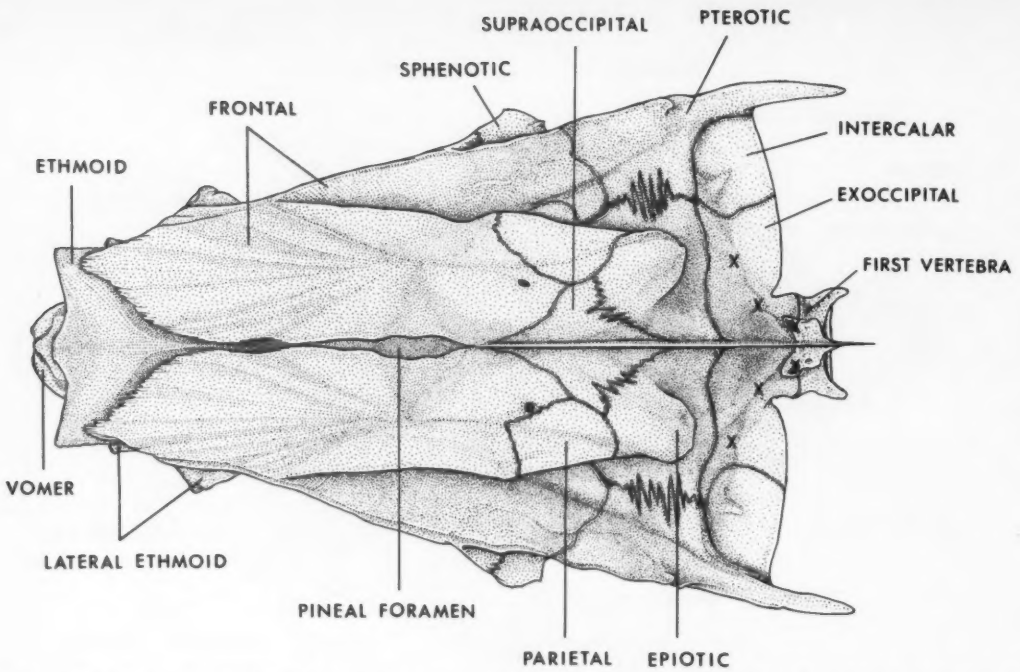


FIGURE 12.–Dorsal view of skull of *Sarda sarda*, eastern United States, 388 mm FL. X's indicate the points of attachment of intermuscular bones.

(Mago Leccia 1958), *Katsuwonus*, and *Thunnus*. In *Cybiosarda* and *Orcynopsis*, these anterofrontal crests are merely visible laterally as in *Auxis* and *Euthynnus*. No anterofrontal crest is present in *Gymnosarda* and *Allothunnus* (Figures 22, 24) and it is also absent in *Grammatorcynus* and *Acanthocybium*.

The first vertebral centrum has modified neural prezygapophyses (Figure 25) that firmly attach the first vertebra to the modified exoccipital and basioccipital region (Figure 26) of the skull. The anterior circular margin of the first centrum is smaller than its posterior margin and is in a forward oblique position to meet the posterior margin of the modified basioccipital which is in a backward oblique position. The strong first neural spine, with its tubular base, sits on the junction of the first centrum and exoccipital and it is not fused to the first centrum. No bony shelf is present in the neural canal (Figure 25a) to divide it into dorsal and ventral portions as is the case in *Auxis*, *Euthynnus*, and *Katsuwonus*. An intermuscular bone is attached to the center of each exoccipital in the bonitos (also see section on ribs and intermuscular bones) except in species of *Sarda* (Figure 26) which have an additional pair of intermuscular bones attached to the exoccipital just anterior to the first neural prezygapophyses and *Gymnosarda* which lacks cephalic intermuscular bones.

The prootic pits (Godsil 1954) of the more advanced scombrids are incipient in bonitos except in *Allothunnus*, which has a larger pouchlike concavity on each side of the ventral surface of the cranium. Part of the roof, floor, and sides of the prootic pit are formed by the prootic and pterotic bones. The branchial musculature originates in these pits in *Thunnus* (Gibbs and Collette 1967). The posterior end of the orbital region extends into a deep median depression, the posterior myodome, which is surrounded by the prootic anterodorsally, the parasphenoid ventrally, and the basioccipital postdorsally and postlaterally, and then opens at the back of the skull between the posterior flanges of the parasphenoid, or communicates with a posterior or parasphenoidal chamber (Kishinouye 1923). The rectus muscles of the eyes attach in the posterior myodome (Gibbs and Collette 1967).

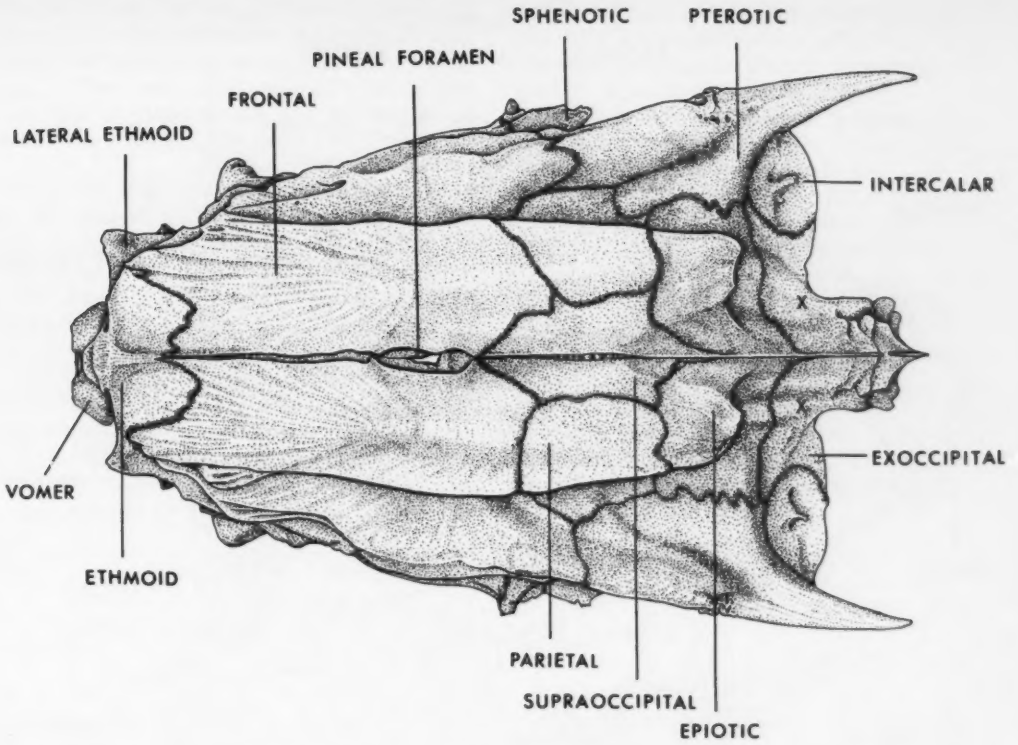


FIGURE 13.–Dorsal view of skull of *Cybiosarda elegans*, Western Australia, 422 mm FL. X's indicate the points of attachment of intermuscular bones.

ETHMOID REGION.–This region is composed of the ethmoid, lateral ethmoid, and vomer. The nasal bone lies lateral to the ethmoid and lateral ethmoid and, therefore, is included here.

Ethmoid.–The ethmoid (dermethmoid) is the most anterodorsally located bone of the neurocranium. It has a smooth flat dorsal surface, slightly convex at the median posterior end, to receive the frontal bones. It connects ventrally to the vomer and posteriorly to the lateral ethmoids with rough and porous sutures. The anterior border of the ethmoid is nearly straight in *Orcynopsis* (Figure 14), but is concave in the other genera with an anteromedian projection and an anterolateral horn on each side.

Lateral Ethmoid.–The paired lateral ethmoids (parethmoids) form the posterolateral wall of the ethmoid region and the anterior wall of the orbit with an olfactory foramen on each side. The lateral ethmoid articulates with the ethmoid anterodorsally, with the frontal bone posterodorsally, with the parasphenoid posteroventrally, and with the vomer anteroventrally. The posterolateral process of the lateral ethmoid serves as an articulating surface for the lachrymal, ectopterygoid, and the entopterygoid. In ventral view, this articulating surface area is small in *Cybiosarda*, slightly larger in *Allothunnus*, and most expanded in the species of *Sarda*, (Figures 15, 18, 19). In *Orcynopsis* and *Gymnosarda*, it is an elongate narrow strip (Figures 16, 17). The lateral expansions of the lateral ethmoids in bonitos resemble those of more primitive scombrids in being wider than in more advanced genera.

Vomer.–The vomer is the most anteroventrally located bone of the cranium. It is located beneath the ethmoid and the lateral ethmoids. Its pointed posterior end fits into the V-shaped anterior projection of the parasphenoid to form the sup-

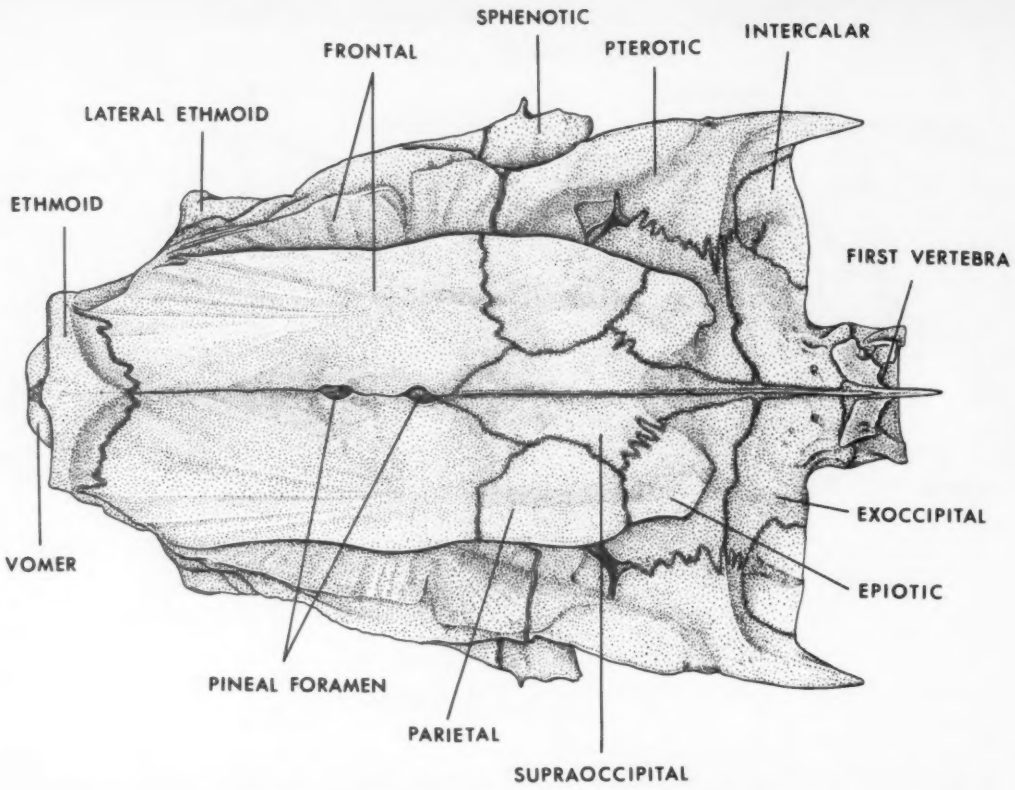


FIGURE 14.—Dorsal view of skull of *Orcynopsis unicolor*, Tunisia, 543 mm FL.

porting axis of the roof of the mouth. Ventrally, the vomer of *Cybiosarda* and *Orcynopsis* (Figures 15, 16) has a blunt anterior edge and bears a patch of villiform teeth. *Sarda australis* and *S. sarda* frequently have a few small teeth on the middle of the expanded part of the vomer, but vomerine teeth are absent in the other bonitos. Some specimens of *S. chiliensis* have a ridge along the midline of the vomer but most have this area flat or convex. The variation is individual, not geographic: 3 of 12 southeastern specimens have a ridge; 6 of 26 northeastern specimens have a ridge. Godsil (1955) mentioned that the ventral surface of the expanded portion of the vomer was flat in Indo-West Pacific *S. orientalis* and that of eastern Pacific specimens was slightly cupped or concave ventrally. We found that this character is not consistent in our material. The anterolateral edges of the vomer are prominent and project ventrally in *Gymnosarda*. The anterior one-third of the vomer in *Allothunnus* projects ventrally with an axelike anterior end and is porous in the middle of the ventral surface. The pointed posterior end of the vomer is more elongate in *Sarda* than in other genera of bonitos.

The bonitos fall into three groups based on vomerine dentition. *Allothunnus*, *Sarda orientalis*, and *S. chiliensis* lack vomerine teeth. A few small teeth are frequently present on the head of the vomer in *S. sarda* and *S. australis* and sometimes in *Gymnosarda*. Both *Orcynopsis* and *Cybiosarda* have a small patch of teeth on the head of the vomer and a few teeth usually extend posteriorly a short distance on the shaft of the vomer.

Nasal.—The anterior end of the nasal, which reaches the premaxilla posterodorsally, is thickened in all bonitos and has an expanded hammerlike head except in the species of *Sarda* (Figure 27). The nasal gradually becomes thinner

towards its posterior margin which attaches to the frontal bone. *Gymnosarda* has the strongest nasal bone, with serrations along its anteroventral margin. The nasal in *Allothunnus* is more elongate than in other bonitos and its constricted midportion is more prominent.

ORBITAL REGION.–The orbit is surrounded by the posterior wall of the lateral ethmoid, the ventral side of the frontal, the pterosphenoid, sphenotic, prootic, suborbital, and lachrymal bones. The left and right orbits are partially separated by the basisphenoid. The sclerotic bones enclose the eyeballs.

Godsil (1955) found a difference in the ratio of orbit height to length between southeastern and northeastern populations of *Sarda chiliensis*. The ratio in his material varied from 5.83 to 6.83 in 5 southeastern specimens (606-659 mm FL) and from 3.40 to 4.50 in 6 northeastern specimens (439-563 mm FL). Following Godsil's definitions, length was measured along the shaft of the parasphenoid, from its juncture with the lateral ethmoid to the point where the lateral wing of the parasphenoid begins. Orbit height is the least distance between the anterior ventral projection of the pterosphenoid and the shaft of the parasphenoid. The range of variation in this ratio (Table 4) indicates that this is not a useful diagnostic character within the genus *Sarda*, although the means for the populations of *S. chiliensis* show the same trend that Godsil found. *Orcynopsis* and *Cybiosarda* have the highest ratios, which indicate the most elongate and narrow orbits and the most ventrally projecting pterosphenoids. *Allothunnus* and *Gymnosarda* have the lowest ratios due to their slightly higher arched orbits and the smooth ventral margins of the pterosphenoids.

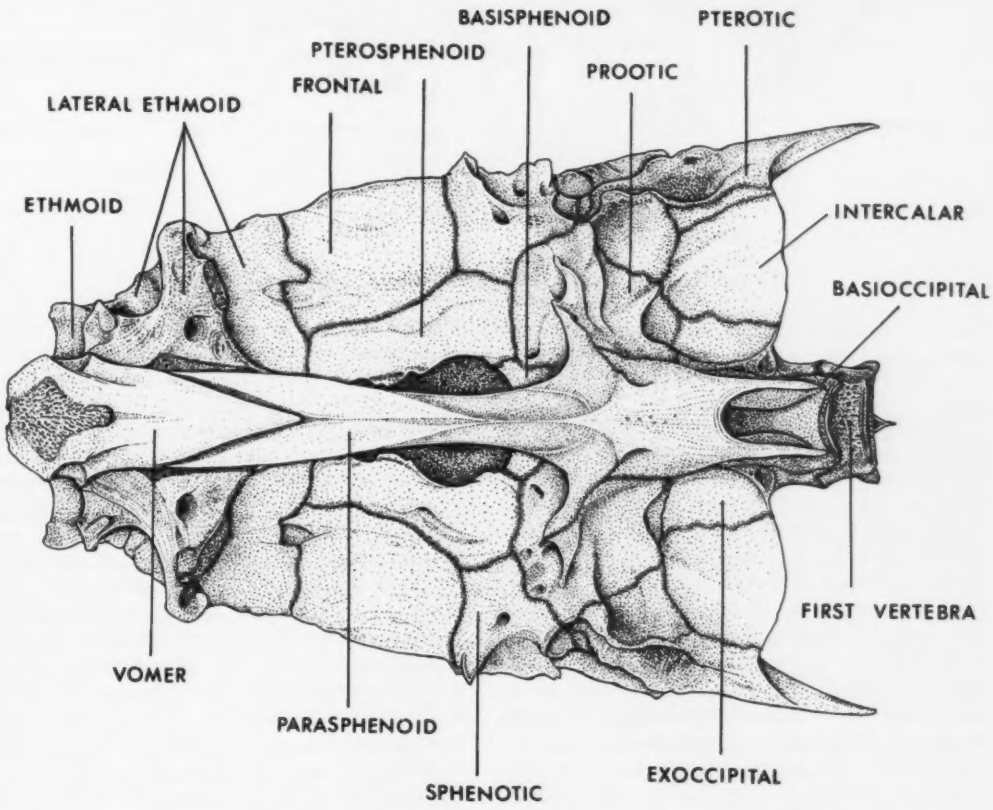


FIGURE 15.–Ventral view of skull of *Cybiosarda elegans*, Western Australia, 422 mm FL.

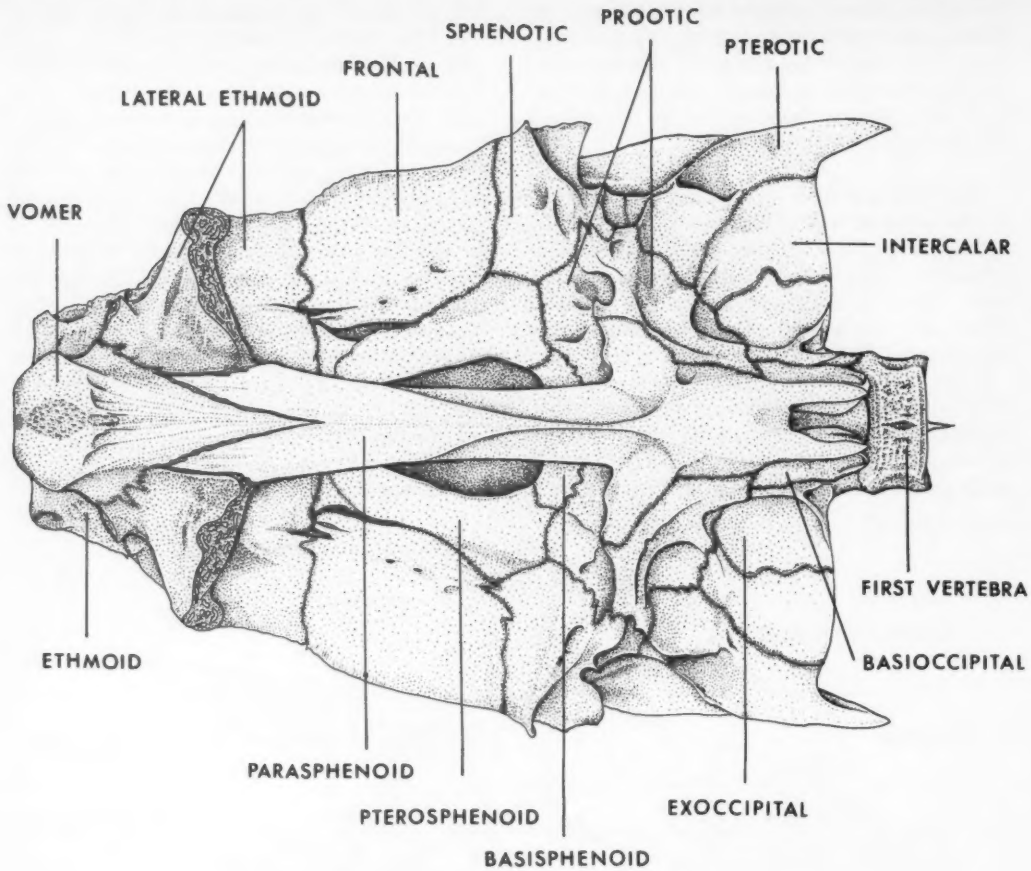


FIGURE 16.—Ventral view of skull of *Orcynopsis unicolor*, Tunisia, 543 mm FL.

Frontal.—Most of the dorsal surface of the cranium is covered by large concave frontal bones. In dorsal view, the anterior ends of the frontals overlap the posterior part of the ethmoid. Posteriorly, they articulate with the sphenotic, pterotic, parietal, and supraoccipital bones. The frontal bones are thickened laterally to form the roof of the orbit; they become thinner where they meet along the median line of the skull and form a crest. A thin bony inner lateral crest begins at the middle of each frontal bone and continues along the parietal to the epiotic bone. A pineal foramen is present immediately anterior to the supraoccipital crest. The pineal foramen is slitlike and filled with cartilage in most bonitos. *Allothunnus* has the largest and thickest frontal bones; they are concave dorsally, with deep conspicuous radiating ridges and lack a frontal crest. A deep round depression, lined with bony ridges, is present anterior to the oval pineal foramen. This feature of *Allothunnus* is similar to that in *Acanthocybium* (Conrad 1938). *Grammatorcynus* also has many conspicuous shallow radiating ridges on the frontal bones. In ventral view, the frontal bone articulates with the lateral ethmoid anteriorly, the pterosphenoid medially, and the sphenotic posteriorly. The ratio of the length of the external edge of the frontal bone to the length of the skull (anterior edge of the vomer to the articulation of the first centrum) varies from 30.9 to 33.3% in *S. australis* (3 specimens 363-495 mm FL) and thus differs from other species of *Sarda*, whose ratios were less than 28%. Laterally, the frontal bone divides into two shelves posteriorly

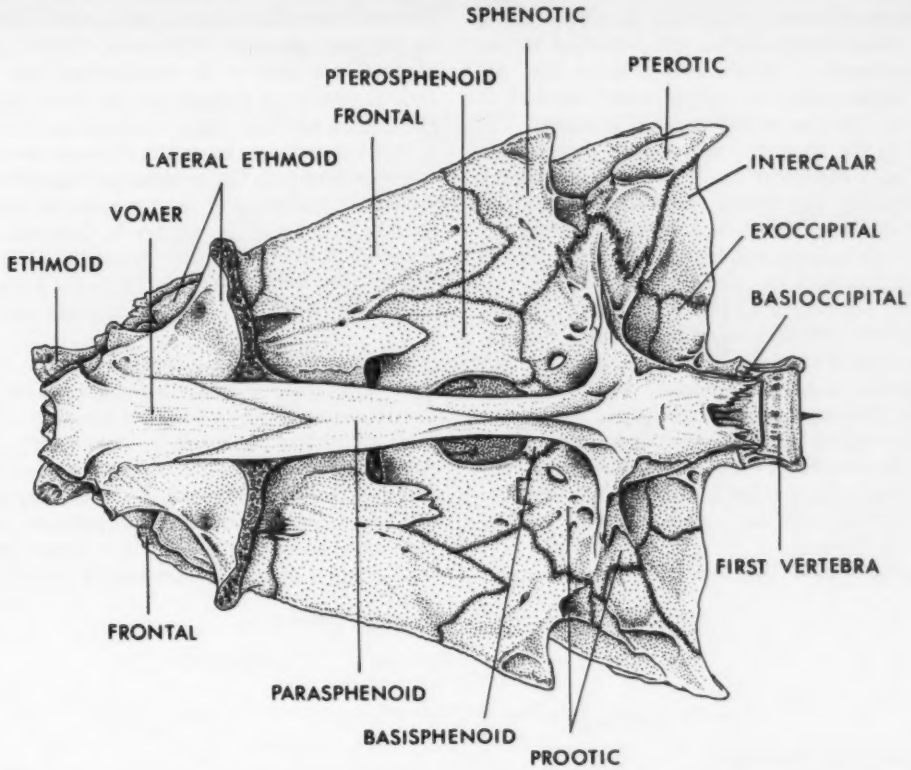


FIGURE 17.—Ventral view of skull of *Gymnosarda unicolor*, Truk Islands, 696 mm FL.

where the upper shelf meets the pterotic and the lower shelf meets the sphenotic. The frontal crest is absent in *Allothunnus* (Figure 24), indistinct in *Cybiosarda*, *Orcynopsis*, and *Gymnosarda* (Figures 20-22), and is most prominent in the species of *Sarda* (Figure 23).

Basisphenoid.—The basisphenoid is a Y-shaped bone, connected dorsally to the prootics and the pterosphenoids. In anterior view, the basisphenoid bisects the entrance of the myodome, with an anteriorly and a posteriorly directed process in its upper half (Figures 20-24), except in *Allothunnus* (Figure 25). Ventrally, the basisphenoid extends toward the parasphenoid to which it is connected in all the bonitos except *Allothunnus*.

Godsil (1954) studied possible differences between the basisphenoids of eastern Pacific *Sarda chiliensis* and *S. orientalis*. He concluded that the lower portion of the basisphenoid in *S. chiliensis* is generally a narrow bone, only slightly expanded, and firmly ankylosed to the parasphenoid. In *S. orientalis*, the lower extremity of the basisphenoid is greatly expanded and it is apparently only loosely attached to the parasphenoid. We agree with his statements in part. In *S. orientalis* from the eastern Pacific and the Indo-West Pacific, the lower extremities of the basisphenoid are expanded and firmly attached to the parasphenoid. In northeast and southeast populations of *S. chiliensis*, the lower portions of the basisphenoid are narrow or slightly expanded and are either firmly or loosely ankylosed to the parasphenoid. In general, the lower extremities of the basisphenoid in *S. chiliensis* are less expanded and less firmly attached to the parasphenoid than in *S. orientalis*.

The angle of the long axis of the basisphenoid relative to the parasphenoid in bonitos is less variable than in *Thunnus* (Gibbs and Collette 1967), but no specific differences were found among the bonitos, except in *Allothunnus*. The

basisphenoid curves posteriorly as it approaches the parasphenoid and is not attached to the parasphenoid in *Allothunnus* (Figure 25). This may explain why the basisphenoid was lost in three of the four skulls that we prepared. The angle of the anterior basisphenotic process was used as a character in *Thunnus* by de Sylva (1955:32-35), but Gibbs and Collette (1967:73) found it too variable to be useful. In bonitos, the axes of the anterior and the posterior processes of the basisphenoid are straight, with the anterior process slightly directed downward in some specimens. *Allothunnus* has no basisphenotic process and the anterior process in *Orcynopsis* and *Cybiosarda* is not as prominent as in the other bonitos. The angle between the axis of the process and the vertical axis of the basisphenoid is similar in all bonitos except for *Gymnosarda* (Figure 19). In *Gymnosarda*, a ridge is present along the axis of the process and the posterior process is more ventrally directed.

Among other scombrids, *Thunnus* and *Scomberomorus* lack a prominent posterior process on the basisphenoid (Gibbs and Collette 1967; Mago Leccia 1958, pl. 3), *Allothunnus* and *Rastrelliger* have no process on the basisphenoid (Nakamura and Mori 1966; Gnanamuttu 1971, fig. 1), *Acanthocybium*, *Auxis*, *Euthynnus*, and *Katsuwonus* have both the anterior and the posterior process. If the shape of the basisphenoid bone is used as a diagnostic character in scombrid classification (Kishinouye 1923; Godsil 1954; de Sylva 1955; Gibbs and Collette 1967), its high intraspecific variability must be taken into account.

Pterosphenoid.–The pterosphenoid (alisphenoid) articulates with the edges of the frontal, sphenotic, prootic, and basisphenoid on the ventral surface of the brain case. Anteriorly, the pterosphenoids are connected to the lateral ethmoids directly or indirectly by a cartilaginous membrane. The paired pterosphenoid bones meet each other anteriorly along the median ventral line forming a pterosphenotic window that differs

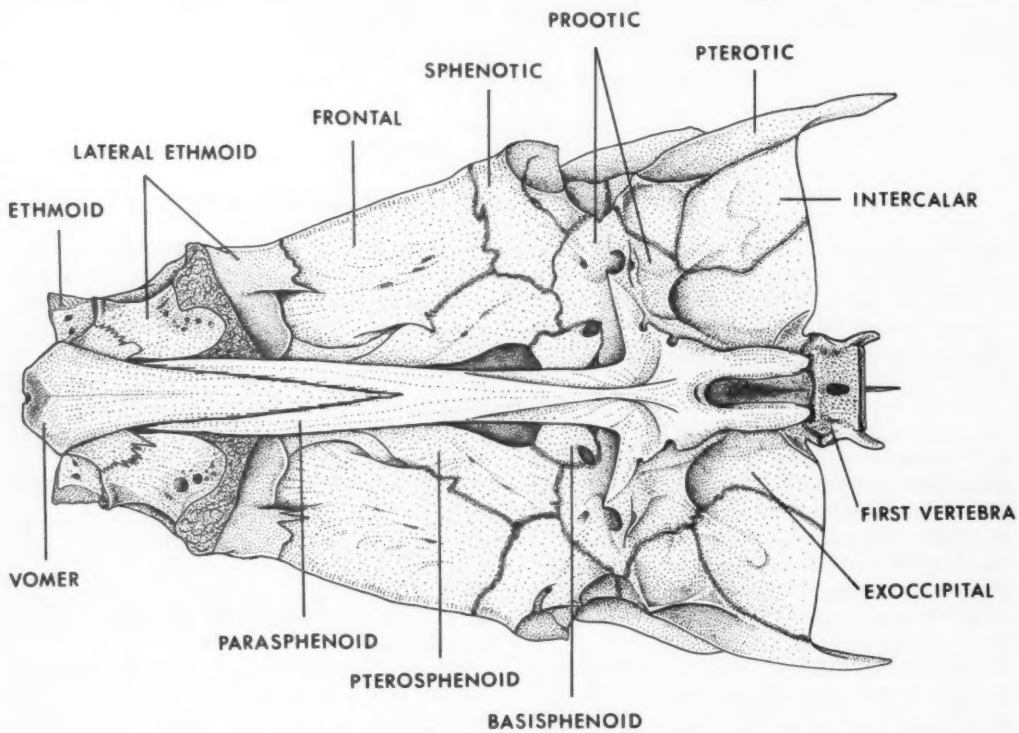


FIGURE 18.–Ventral view of skull of *Sarda sarda*, eastern United States, 388 mm FL.

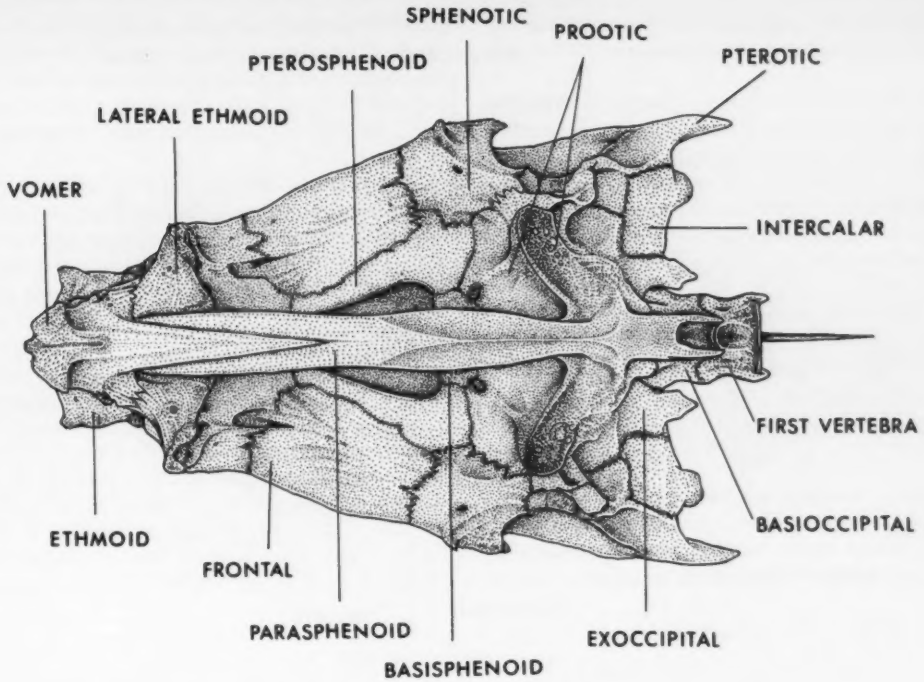


FIGURE 19.—Ventral view of skull of *Allothunnus fallai*, California, 680 mm FL.

slightly among the bonitos in shape. *Cybiosarda*, *Orcynopsis*, and *Gymnosarda* have a beer bottle-shaped window; it is roughtly triangular with a broad arched posterior margin in *Sarda*. In *Allothunnus*, a thin bony membrane is present along the inner edge of the pterosphenoid toward the center of the window. The pterosphenoids do not fuse with the parasphenoid, as they frequently do in large specimens of *Thunnus thynnus* (Gibbs and Collette 1967).

Lachrymal.—The lachrymal is an elongate bone that covers up part of the maxilla and is attached to the lateral ethmoid by means of a dorsal projection on its inner surface (Figure 9). This process is most pronounced in *Gymnosarda* and most flattened in *Allothunnus*. The anterior margin of the lachrymal has an indentation with an anteriorly projecting process on the dorsal margin of the indentation (Figure 28). The margin is slightly concave in *Sarda* and *Gymnosarda* compared to the deep notch present in the other bonitos, *Cybiosarda* has the longest anterior process, much longer and thinner than in *Orcynopsis*. *Gymnosarda* has a wide blunt process. The lachrymal is relatively shorter and stronger in *Gymnosarda* and it is extremely heavy and sculptured at the dorsal projection and along the posterodorsal margin.

Suborbital bones.—Nakamura and Mori (1966) stated that the first and second suborbital bones are inconspicuously developed and not much differentiated from the scales on the cheek in *Allothunnus*. Suborbital bones are present in the bonitos, but we have made no special effort to study them.

Sclerotic.—The sclerotic bones consist of two thickened semicircular segments connected by cartilage on the inner lateral surface and by corneal membranes on the outside. The inner rim of the sclerotic bones appears elliptical externally in all bonitos as in *Thunnus atlanticus* (de Sylva 1955, fig. 7).

OTIC REGION.—This region encloses the otic chamber inside the skull, and is formed by the

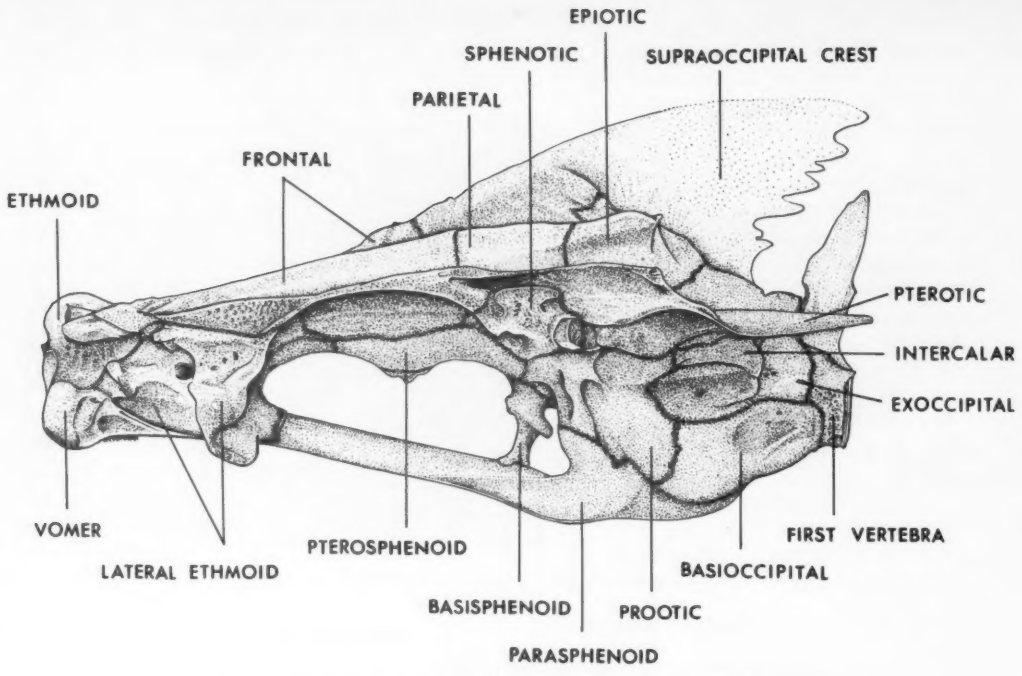


FIGURE 20.—Lateral view of skull of *Cybiosarda elegans*, Western Australia, 422 mm FL.

parietal, epiotic, supraoccipital, pterotic, prootic, sphenotic, and intercalar (opisthotic) bones.

Parietal.—The parietal articulates with the frontal anteriorly, the supraoccipital and the pterotic laterally, sphenotic ventrally, and epiotic posteriorly. The inner lateral crest that originates at the middle of the frontal bones continues through the parietals to terminate at the epiotics. This crest is typical of scombrids but is less developed in *Grammatorcynus* and in *Scomber* (Allis 1903).

Epiotic.—The epiotic is massive, irregular, and bounded by the parietal anteriorly, the supraoccipital mediolaterally, the exoccipital posteriorly, and the pterotic distolaterally. The inner lateral crest terminates at the posterior end of the epiotic. The medial process of the posttemporal bone is also attached here. The epiotic bones of all the bonitos are similar.

Supraoccipital.—The supraoccipital can be divided into two parts: a thin, elongate triangular crest and a roughly hexagonal shaped base. The supraoccipital crest arises just behind the pineal foramen and extends posterodorsally. In bonitos, the crest extends posteriorly over the first neural spine but usually not over the posterior margin of the first centrum. In *Allothunnus* the crest extends posteriorly over the second centrum. In dorsal view, the hexagonal base articulates with the frontal bones anterolaterally, the parietals laterally, and the epiotic posteriorly. *Cybiosarda* and *Orcynopsis* have the narrowest and most elongate supraoccipital base; *Allothunnus* has the shortest and widest.

Pterotic.—Dorsally, the pterotic is the most posterolaterally located bone. The pterotic articulates with the epiotic and parietal medially and with the exoccipital and intercalar posteriorly. A sharp posteriorly pointed process is characteristic of the pterotic bone of the bonitos as well as other scombrids. In ventral view, the pterotic articulates with the sphenotic anteriorly and the prootic and intercalar medially. Two fossae, one at the posterior half of the pterotic bone and one at its joint with the sphenotic, seat the dorsal and anterior condyles of the hyomandibula. A deep

depression continues from the interspace of the posterior frontal shelves and separates the pterotic from the sphenotic. In bonitos, the size of both fossae varies only slightly; they tend to be deeper and larger in *Gymnosarda* and *Allothunnus*.

Prootic.–In ventral view, the prootic connects with all ventral bones which compose the posterior part of the neurocranium (Figures 15-19). The prootic bones are irregular in shape and meet each other along the ventral median line of the brain case to form the anterior portion of the posterior myodome. A prootic foramen is present anterolaterally between the tip of the parasphenoid wing and the sphenotic. The strut forming the outer part of the foramen is absent in *Allothunnus* forming a deep groove. The prootic pit of the more advanced scombrids (Gibbs and Collette 1967) is present in *Allothunnus* and absent or incipient in the other bonitos. In addition to the distinct prootic pit in *Allothunnus*, there is a very peculiar thick bony wing which is developed laterally; this twisted wing has a smooth convex anterior surface and a concave posterior surface.

Sphenotic.–The sphenotic bone forms the most posterior dorsolateral part of the roof of the orbit. It forms a continuation of the outer lateral shelf from the frontal bones and articulates with the pterosphenoid medially and the prootic and pterotic posteriorly. The lateral process of the sphenotic serves as an attachment for the outer process of the supratemporal. This process is pointed in *Cybiosarda*, *Orcynopsis*, *Gymnosarda*, and *Allothunnus*, and is less sharp in the species of *Sarda*. There are differences in the outlines of the joints around the sphenotic bone with the adjacent bones, but these are probably individual variations.

Intercalar.–The intercalar (opisthotic) bone fits between the pterotic and exoccipital bones (Figures 10-14) and bears a dorsal protuberance which connects to the lateral process of the post-

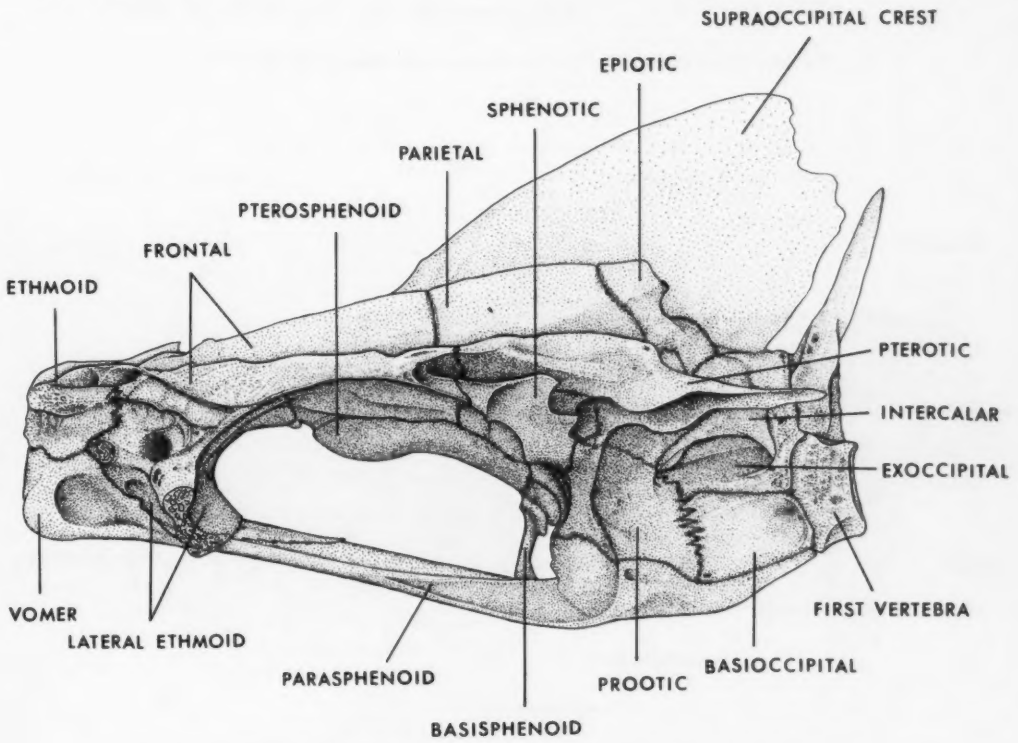


FIGURE 21.–Lateral view of skull of *Orcynopsis unicolor*, Tunisia, 543 mm FL.

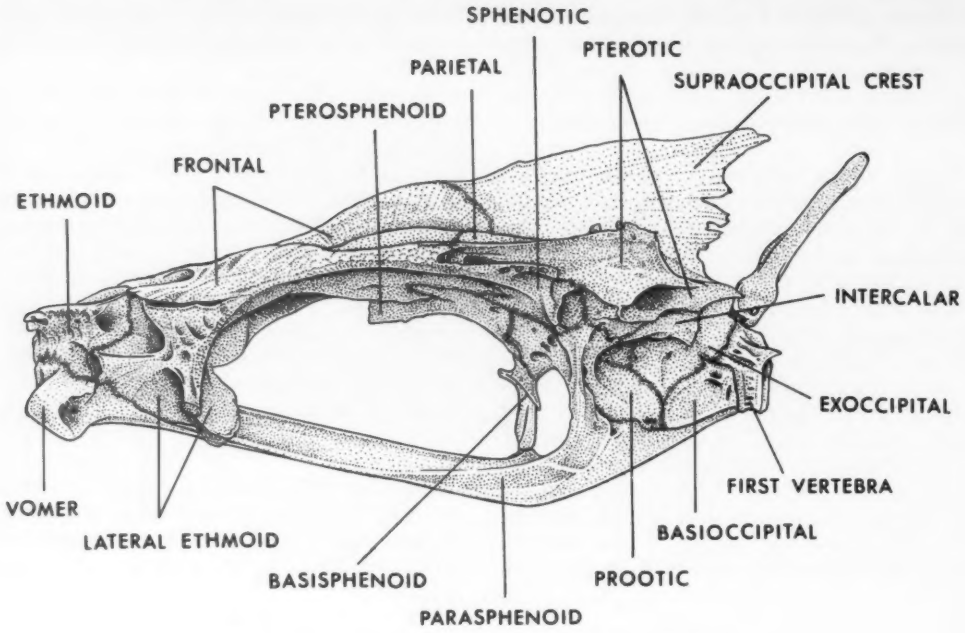


FIGURE 22.—Lateral view of skull of *Gymnosarda unicolor*, Truk Islands, 696 mm FL.

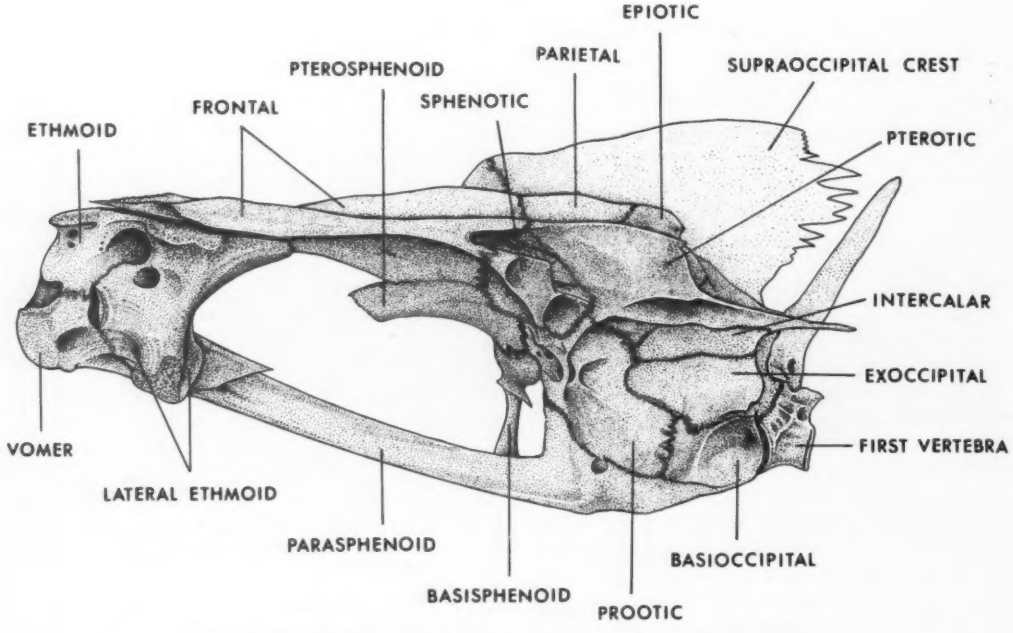


FIGURE 23.—Lateral view of skull of *Sarda sarda*, eastern United States, 388 mm FL.

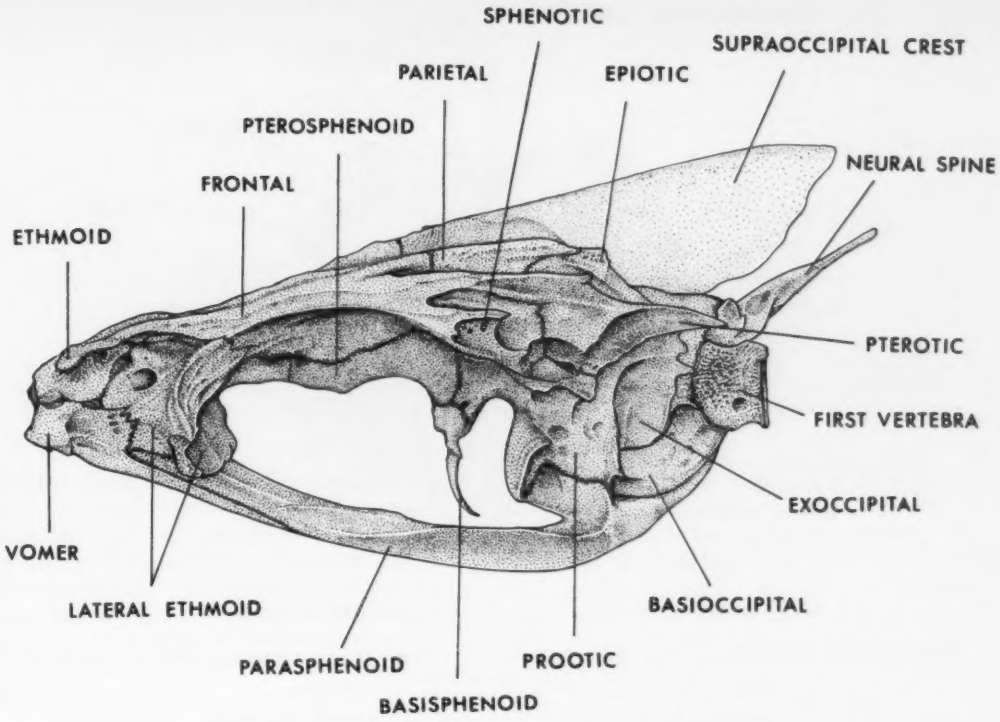


FIGURE 24.—Lateral view of skull of *Allothunnus fallai*, California, 680 mm FL.

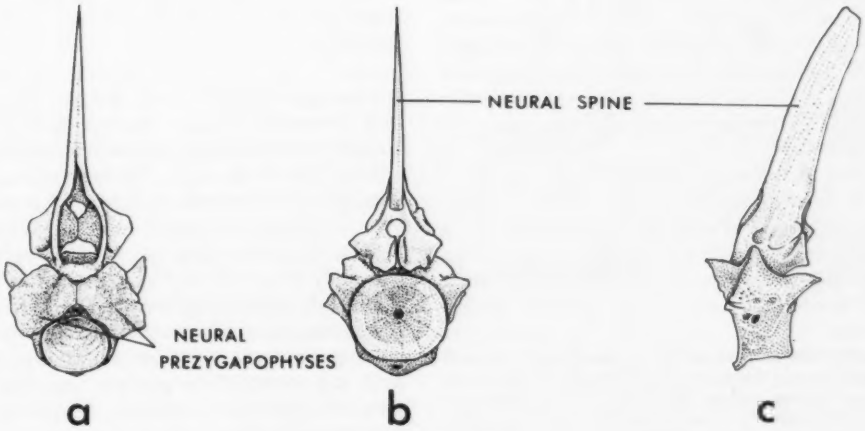


FIGURE 25.—First vertebra of *Sarda chiliensis*, Callao, Peru, 571 mm FL. a. Anterior view. b. Posterior view. c. Lateral view.

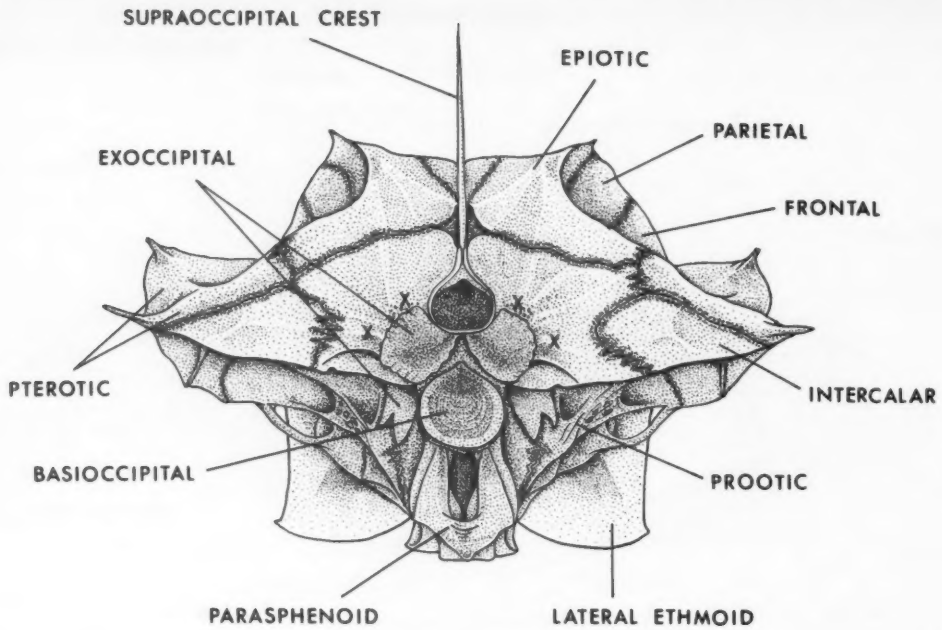


FIGURE 26.—Rear view of skull of *Sarda chiliensis*, Callao, Peru, 571 mm FL. X's indicate the points of attachment of intermuscular bones.

temporal. In *Allothunnus*, this protuberance projects out from the posterior outline of the skull, while in other bonitos this outline is smooth. Ventrally, the intercalar articulates with the prootic bone anteriorly and the exoccipital and pterotic bones laterally (Figures 15-19).

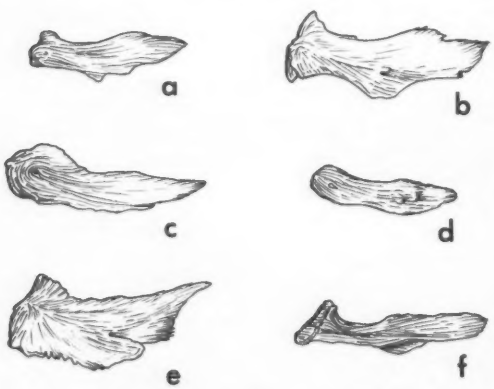


FIGURE 27.—Nasals of six species of Sardini, left external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda chiliensis*, Callao, Peru, 442 mm FL. d. *Sarda sarda*, Florida, 333 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, Tasmania, 775 mm FL. a-d drawn twice as large as e and f.

BASICRANIAL REGION.—This region consists of the parasphenoid, basioccipital and exoccipital bones, and forms the posteroventral base of the skull.

Parasphenoid.—Ventrally, the parasphenoid is a long cross-shaped bone (Figures 15-19) which articulates with the vomer anteriorly and forms the ventral axis of the skull. The lateral wing of the parasphenoid extends dorsolaterally along the ventral ridge of the prootic bones on either side and has a pointed end, which forms part of the anteroventral wall of the posterior myodome. Posteriorly, the parasphenoid bifurcates into two lateral flanges which attach dorsally to the corresponding posteroventral flanges of the basioccipital bone and surround the posterior opening of the posterior myodome. A ventrally projecting keel is present along the posterior two-fifths of the parasphenoid. The V-shaped joint connecting the parasphenoid with the vomer anteriorly is most

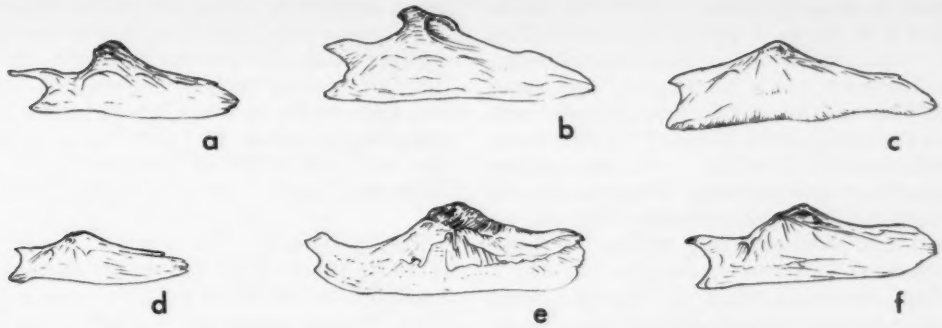


FIGURE 28.–Larchrymals of six species of Sardini, left lateral view. a. *Cybiosarda elegans*, New South Wales, 360 mm FL. b. *Orcynopsis unicolor*, Tunisia, 495 mm FL. c. *Sarda orientalis*, Tokyo, 350 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, California, 680 mm FL. a, b, and c drawn twice as large as d, e, and f.

elongate in *Allothunnus* and the species of *Sarda* (also see vomer). In ventral view, the general characteristic of the parasphenoid is a gradual narrowing of the bone from anterior to posterior. *Orcynopsis* has the widest and strongest parasphenoid; species of *Sarda* have the weakest. Broad parasphenoids are also present in *Scomberomorus* and *Acanthocybium*; narrower parasphenoids in *Auxis*, *Euthynnus*, *Katsuwonus*, and *Thunnus*. The broadest portion of the parasphenoid is usually located at or before the tip of the V-shaped joint with the vomer in all bonitos except *Allothunnus*. In five skulls (406-778 mm FL) of *Allothunnus*, the broadest portion of the parasphenoid is in the posterior half of the bone, about at the beginning of the ventral keel. This is in contradiction to Nakamura and Mori (1966, fig. 4B), whose illustration of a specimen (876 mm FL) shows the parasphenoid as similar to other bonitos.

The anterior edge of the lateral wings of the parsphenoid is smoothly concave forward and forms a dorsolaterally directed shelf, visible ventrally in all bonitos except *Allothunnus*. In *Allothunnus* (Figure 19), the anterior edge of the lateral wing is deeply concave and the wing projects vertically along the prootic wing toward the roof of the skull, as in the more advanced scombrids. The posterior opening, between the lateral flanges of the parasphenoid, is usually elongate and the lateral flange does not extend beyond the juncture of the skull with the first centrum (Figures 15-19). In our *Gymnosarda* skulls, this opening is much smaller than in the other bonitos (Figure 17). A thin layer of bone covers the anterior portion of the opening, perhaps indicating additional ossification in larger individuals of this particular species.

In lateral view (Figures 20-24), the parasphenoid forms the ventral border of the orbit and connects with the lateral ethmoid, basisphenoid, prootic, and basioccipital bones dorsally. The ventral keel projects further ventrally in *Gymnosarda* and *Allothunnus* than in *Orcynopsis* and *Cybiosarda*. The posterior one-third of the parasphenoid and its lateral flanges are strongly convex in *Allothunnus*, forming the unique posteroventral outline of its skull (Figure 24). A middorsal ridge is also present in all bonitos. This ridge arises from the juncture of the lateral ethmoids, where the ridge projects the most, and merges into the main axis of the parasphenoid posteriorly at about the beginning of the ventral keel. Usually, a triangular piece of cartilage, connecting with the lateral ethmoid, covers the most anterior end of the dorsal ridge. The middorsal ridge is least prominent in *Cybiosarda*.

Basioccipital.–The basioccipital is the most posteroventrally located bone of the skull. It is shaped like an inverted U with lateral flanges on either side of the skull and forms the roof and lateral walls of the posterior myodome. Anteriorly, the basioccipital is attached to the prootic bones and dorsally with the exoccipital bones. Its lateral flanges expand ventrally to meet the flat posterior flanges of the parasphenoid. Posteriorly, the lateral flanges fuse to form a circular margin in a slightly backward oblique position and attach to the margin of the first vertebral centrum (Figure 25). In lateral view, a distinct deep concave pit is

present at the posterodorsal corner of the basioccipital in all bonitos (Figures 20-24). Godsil (1954) first noted this feature, "a deep-rimmed, crater-like depression in the basioccipital," and stated that "This character is sufficient to separate *Sarda* from any species of the Plecostei." In 1955, Godsil modified this statement to ". . . it is not a positive diagnostic generic character." In comparing this basioccipital depression with other scombrids, we found it to be diagnostic of bonitos. In *Auxis*, *Euthynnus*, *Katsuwonus*, and *Thunnus* only a shallow concave surface is present; *Scomberomorus* and *Acanthocybium* have small foramina on the corresponding position of the basioccipital. *Grammatorcynus* has a similar depression but it is much shallower.

Exoccipital.–The exoccipitals connect the skull to the first vertebra dorsally. The exoccipital articulates with the epiotic and supraoccipital bones anterodorsally, the intercalar laterally, and with the other exoccipital posterodorsally. In ventral view, the exoccipital articulates with the prootic anteriorly, basioccipital medioventrally, and intercalar laterally. In posterior view, the foramen magnum is framed by the exoccipitals. Dorsally, a small foramen is present at the medioposterior corner of the exoccipital and it opens into the brain cavity. The exoccipital bones are similar, with an intermuscular bone attached, in all bonitos except *Gymnosarda* which has none and *Sarda* which has two (Figure 12).

OTOLITHS.–The first figures of bonito otoliths were presented by Shepherd (1910a, b) who illustrated the asteriscus and sagitta of *Sarda sarda* along with other miscellaneous eastern Atlantic species, but his figures are too small and poorly defined to be of any comparative value. Chaine (1957) published good figures of the sagittae of *Sarda sarda* as well as two species of *Scomber*, two of *Thunnus*, and *Scomberomorus tritor*. Bauzá Rullán (1961:155-156, pl. 1, figs. 7-10) also illustrated the sagitta of *S. sarda*. Two studies include information about intraspecific variation in the shape of bonito sagittae. Chaine (1957) discussed variation in *S. sarda*; Kuo (1970:125, fig. 7) showed considerable variation with outline sketches of sagittae from the left and right sides of 47 *S. chiliensis* from California in an age and growth study. Fitch and Craig (1964) made the first comparative study of scombrid otoliths when they compared the sagittae of eastern Pacific scombrids in an attempt to assess the relationships of *Allothunnus fallai*. They found that scombrid sagittae, except for *Scomber japonicus*, have a long thin rostrum, finely serrate margins, and a deep sulcus on the inner face. Among bonitos, they compared the otoliths of *Allothunnus* and three species of *Sarda* (*chiliensis*, *orientalis*, and *sarda*). *Allothunnus* and *S. chiliensis* were illustrated.

Specific Characters.–We calculated proportions of the sagittae as percent of the otolith (sagitta) length (OL) in fork length and the greatest height (H) in length of sagitta and in length of rostrum (R).

	FL (mm)	*OL*/*FL* (%)	*H*/*OL* (%)	*H*/*R* (%)
Orcynopsis	576	1.54	48.3	1.3-1.4 ($n=3, \bar{x}=1.39$)
Cybiosarda	365	1.56	44.6	1.0-1.2 ($n=4, \bar{x}=1.09$)
Sarda sarda	418	1.17	35.7	0.9
S. orientalis	350	1.10	33.8	0.8
Gymnosarda	789	0.91	44.4	1.2
Allothunnus	775	0.92	44.8	1.2

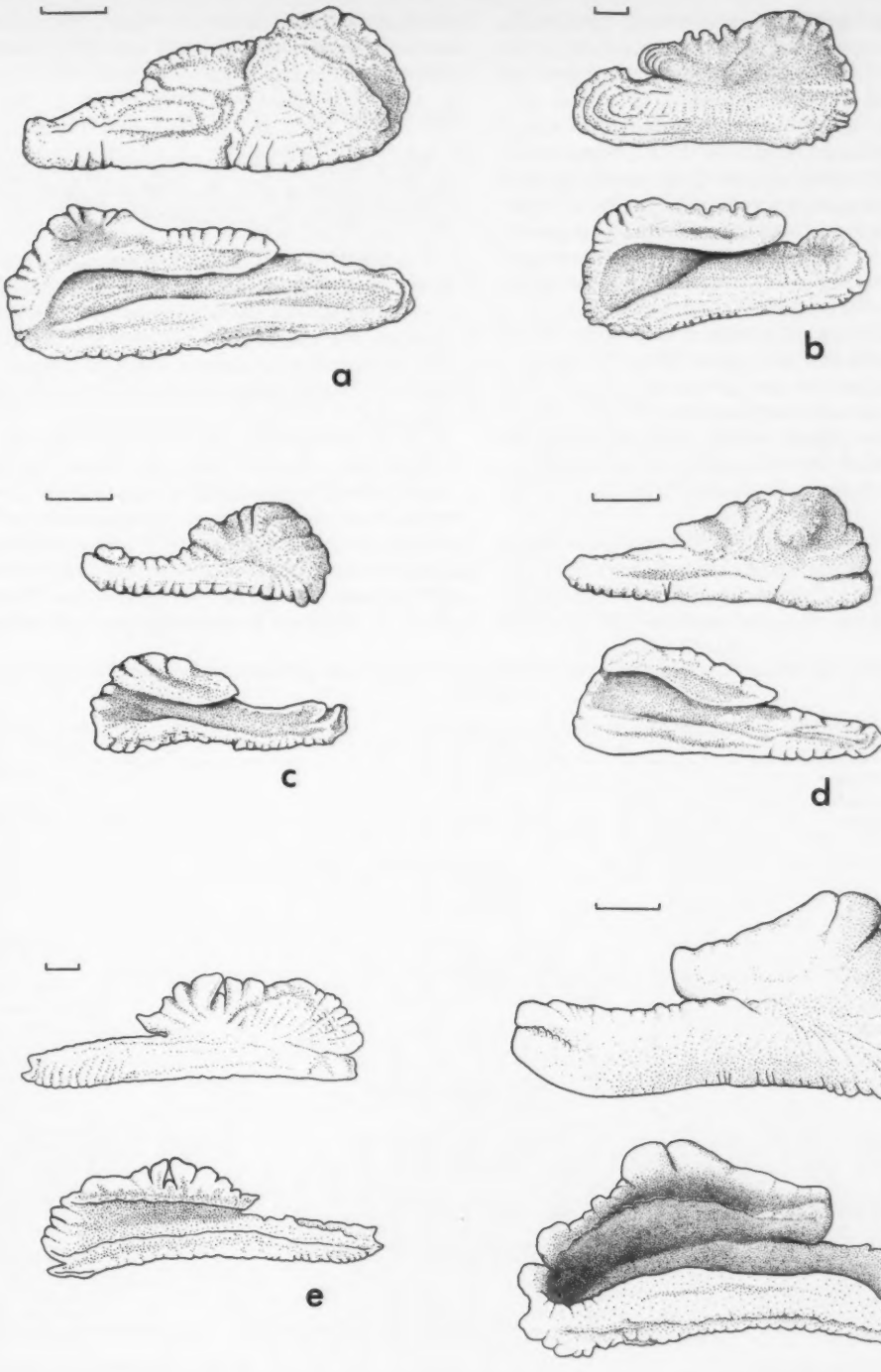
($n=1$ unless otherwise noted)

The sagitta of *Orcynopsis* is the largest among the bonitos relative to fork length. It has a ridge extending from the postdorsal part of the outer surface to the middle of the otolith. It also has the shortest and widest rostrum and the deepest sulcus of any bonito (Figure 29b).

The sagitta of *Cybiosarda* is larger and heavier than *Sarda*. It is similar in size to *Orcynopsis* but has a longer and thinner rostrum. *Cybiosarda* has two ridges extending from the middorsal and posteroventral parts of the sagittae toward the ventral and middorsal areas respectively (Figure 29a). The latter one seems to be weaker. Both *Cybiosarda* and *Orcynopsis* are distinct in having a winglike flange which extends outward and forms a small platform at the posterodorsal margin on the inner side.

The sagittae in the species of *Sarda* are small and have similar outlines (Figure 29c, d). A pyramidlike ridge is present in the middle of the posterior half of the sagitta. They also have the

FIGURE 29.–Sagittae of six species of Sardini, upper figure of each pair is the outer view, lower figure the inner view. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Tunisia, 567 mm FL. c. *Sarda orientalis*, Tokyo, 350 mm FL. d. *Sarda sarda*, Azores, 418 mm FL. e. *Gymnosarda unicolor*, Marshall Islands. f. *Allothunnus fallai*, Tasmania, 775 mm FL. (Scale indicates 1 mm.)


a
b
c
d
e
f

longest and narrowest rostra among bonitos. The dorsal process above the rostrum seems to vary considerably inter- and intraspecifically (see Kuo 1970, fig. 7).

The sagittae of *Gymnosarda* are distinct from those of all other bonitos by their extreme curvature when viewed in situ from above, by their concave ventral margin (sagittae of all other bonitos have relatively straight ventral margins), and by the fact that except for minor protuberances and other irregularities the dorsal margin, in the posterior half of the otolith, roughly parallels the ventral margin, giving a sameness of height to the otolith in this region. The sulcus is more distinctive on the inner surface. The posterior dorsal margin is deeply serrate. No pyramidlike ridge is present in the middle of the posterior half. Laterally, the deepest part of the sagitta is in front of the middle of the posterior half.

The sagitta of *Allothunnus* is small and similar in size to the species of *Sarda*. It has a very distinctive triangular outline; with an acute posteroventral angle and no prominent ridges on the outer surface. The inner surface of the sagitta has a deep sulcus with a very prominent dorsal ridge.

Branchiocranium

The branchiocranium is divided into five sections: mandibular arch, palatine arch, hyoid arch, opercular apparatus, and branchial arch.

MANDIBULAR ARCH.–The mandibular arch is composed of the upper jaw (premaxilla, maxilla, and supramaxilla) and the lower jaw (dentary, angular, and retroarticular). Teeth are borne on the premaxilla and dentary, and the number of teeth on these bones is a useful taxonomic character.

Dentition.–Conical teeth are present on the upper and lower jaws in all bonitos. These teeth differ from the laterally compressed teeth with serrate edges found in Spanish mackerels (Scomberomorini) and are generally larger than the tiny conical teeth of the higher tunas (Thunnini). In addition to jaw and palatine teeth,

TABLE 5.–Number of teeth in the upper jaw in species of Sardini. (Mean of left and right sides rounded off upwards to nearest whole number.)

Species	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	*N*	$\bar{x}$
Cybiosarda elegans		1	2	1	2	1	5	4	4	1	1										22	17.9
Orcynopsis unicolor:																						
E Mediterranean							2	3	2	5	5	5	6	3	2						33	22.2
Cent. Mediterranean								1	—	—	3	—	—	1	1	1					7	23.3
Atlantic										2	—	1	2								5	22.6
Total							2	4	2	7	8	6	8	4	3	1					45	22.4
Sarda australis					2	3	2	7	2	2	1										19	18.7
Sarda chiliensis:																						
NE Pacific									2	9	11	15	16	11	6	2	—	2	2		76	23.7
SE Pacific							3	3	3	—	5	9	7	2	6	2	1				41	23.0
Total							3	3	5	9	16	24	23	13	12	4	1	2	2		117	23.5
Sarda orientalis:																						
Indian Ocean		1	3	—	3	1	2	1													11	15.9
NW Pacific	1	2	2	4	4	1															14	14.8
Cent. Pacific	1	—	1	2																	4	14.0
E Pacific		2	3	1	4	4	3	1	1												19	16.2
Total	2	5	9	7	11	6	5	2	1												48	15.5
Sarda sarda:																						
North America						8	4	18	12	10	6										58	19.5
South America					1	—	—	1	2	2	6	3									15	21.2
NE Atlantic							2	1	—	—	—	—	5	1							9	22.2
Mediterranean-Black Sea					1	1	1	—	5	6	8	5	4								31	21.4
(Demir 1964, Turkey)			(1	2	2	4	17	18	19	12	14	11	11	5	2)						(118)	(20.6)
Gulf of Guinea-S. Africa						3	2	5	4	3	3	5	1								26	20.4
Total					2	12	9	25	23	21	23	13	10	1							139	20.5
Gymnosarda unicolor:																						
Indian Ocean				2	—	4	1	—	—	—	—	—	1	—	1						9	18.4
W Pacific			1	3	3	1	2	3	3	2	—	1	1	—	—	1	—	—	1	1	23	19.8
Total			1	5	3	5	3	3	3	2	—	1	2	—	1	1	—	—	1	1	32	19.4
Allothunnus fallai															(40-42-44-51-54-55)						6	47.7

patches of teeth are present on the vomer and tongue in some genera. *Allothunnus* has many very small teeth (40-55) on each of the upper and lower jaws, compared to a range of 12-31 on the upper jaw and 10-25 on the lower jaw in other bonitos (Tables 5, 6). *Orcynopsis* averages more teeth in both upper and lower jaws than does *Cybiosarda*. Both *Gymnosarda* and *Sarda australis* have a very wide range in the number of jaw teeth. In the eastern Pacific, the tropical *Sarda orientalis* differs from the south and north temperate *S. chiliensis* in having fewer upper (13-20, $\bar{x}$ 16.2 vs. 18-30, $\bar{x}$ 23.5) and lower (10-17, $\bar{x}$ 13.2 vs. 14-25, $\bar{x}$ 19.2) jaw teeth. Numbers of jaw teeth and gill rakers are correlated: note especially *Allothunnus* with 70-80 gill rakers and *Orcynopsis* with more gill rakers than *Cybiosarda* (Table 7).

Premaxilla.–The premaxilla (Figure 30) is a long curved bone with a stout arrowhead-shaped anterior end and teeth on the ventral margin. The angle between the oblique anterior and the ventral margin of the premaxilla is most acute in *Gymnosarda* and *Orcynopsis*, similar to *Scomberomorus*. It is almost perpendicular with a small anterior projection in *Allothunnus* (Figure 30f), as in *Thunnus*. The sharp anterior dorsal process of the premaxilla in the species of *Sarda* separates them from the other bonitos (Figure 30c, d). The posterior end of the premaxilla in *Allothunnus* is also similar to *Thunnus*, sharper and thinner than in the other bonitos. The main axis of the premaxilla is curved more in *Gymnosarda*, *Cybiosarda*, and *Orcynopsis* than in *Sarda* and *Allothunnus*.

Maxilla.–The maxilla (Figure 31) is a long curved bone with two irregularly shaped condyles which join the premaxilla anterodorsally. The main axis of the maxilla is most curved in *Orcynopsis* and most flattened in *Gymnosarda* and *Allothunnus* (as in *Thunnus*). A process from the lower condyle of the anterior portion of the maxilla protrudes ventrally in *Cybiosarda* and the species of *Sarda*. This projection is not present in *Scomberomorus* or *Thunnus*. The posterior ends of the maxillae of *Gymnosarda* and *Allothunnus* are broader than in other bonitos. The anterior ends of

TABLE 6.–Number of teeth in the lower jaw of species of Sardini. (Mean of left and right sides rounded off upwards to nearest whole number.)

Species	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	*N*	$\bar{x}$
Cybiosarda elegans	2	1	7	8	1	1	2	1									23	13.0
Orcynopsis unicolor:																		
E Mediterranean			1	1	2	3	6	3	9	5	1	2					33	17.1
Cent. Mediterranean							1	1	2	1							5	17.6
Atlantic						1	—	1	1	1	1						5	17.8
Total			1	1	2	4	7	5	12	7	2	2					43	17.2
Sarda australis		1	2	2	5	5	2	1	—	—	1						19	14.5
Sarda chiliensis:																		
NE Pacific						2	2	7	18	16	9	10	8	2	1	2	77	19.4
SE Pacific					1	3	4	5	8	7	4	2	5	4			43	18.9
Total					1	5	6	12	26	23	13	12	13	6	1	2	120	19.2
Sarda orientalis:																		
Indian Ocean		2	4	3	—	2											11	12.6
NW Pacific		2	3	5	3	1											14	12.9
Cent. Pacific				3	1												4	13.3
E Pacific	2	1	3	6	2	3	1	1									19	13.2
Total	2	5	10	17	6	6	1	1									48	13.0
Sarda sarda:																		
North America			3	4	12	18	15	3	2	1							58	15.0
South America					2	2	4	3	3								14	16.2
NE Atlantic						1	—	4	—	1	2	—	—	—	1		9	18.4
Mediterranean-Black Sea				1	2	4	6	3	10	4	1						31	16.9
(Demir 1964, Turkey)			(1	6	9	21	18	22	18	16	3	3	1)				(118)	(16.7)
Gulf of Guinea-S. Africa				1	5	3	7	6	2	2							26	16.0
Total			3	6	21	28	32	19	17	8	3	—	—	—	1		138	16.0
Gymnosarda unicolor:																		
Indian Ocean	1	—	2	4	—	—	—	1	—	1							9	13.5
W Pacific	2	5	4	3	4	1	1	1	—	—	—	1	1	—	1		24	13.9
Total	3	5	6	7	4	1	1	2	—	1	—	1	1	—	1		33	13.8
Allothunnus fallai													(41-42-49-53)				4	46.3

TABLE 7.–Total number of gill rakers on the first arch in species of Sardini.

Species	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	N	$\bar{x}$
Cybiosarda elegans					3	12	4	1													20	13.2
Orcynopsis unicolor:																						
E. Mediterranean						1	8	18	8	1											36	15.0
Cent. Mediterranean					1	—	1	3	1												6	14.5
(Postel 1956a, Tunisia)						(2	51	96	34	6)											(189)	(15.0)
Atlantic							1	4	1												6	15.0
Total					1	1	10	25	10	1											48	14.9
Sarda australis												3	10	5							18	20.1
Sarda chiliensis:																						
NE Pacific																3	9	12	10	6	40	25.2
(Kuo 1970)															(1	28	226	229	25	1)	(510)	(24.5)
SE Pacific																3	4	9	10	3	29	25.2
(Kuo 1970)																(6	41	44	1)		(92)	(24.4)
Total																6	13	21	20	9	69	25.2
Sarda orientalis																						
Indian Ocean			2	4	2	1															9	11.2
NW Pacific		2	4	3	1	1															11	10.0
Cent. Pacific			4																		4	10.0
E Pacific	1	—	2	7	4	3															17	11.3
Total	1	2	12	14	7	5															41	11.0
Sarda sarda:																						
North America									6	25	14	7	2	—	1						55	17.6
South America										2	6	2	2	2							14	18.7
NE Atlantic											3	—	4	4							11	19.8
Mediterranean-Black Sea											1	5	7	5	12	2					32	20.9
(Demir 1964, Turkey)									(1	2	31	172	427	247	112	7	1)				(1,000)	(20.3)
Gulf of Guinea-S. Africa											1	1	11	4	10	1					28	20.9
Total									6	27	25	15	26	15	23	3					140	19.3
Gymnosarda unicolor:																						
Indian Ocean						3	4	1													8	12.7
W Pacific				1	7	13															21	12.6
Total				1	10	17	1														29	12.6
Allothunnus fallai																	(72-73-74-75-76-80)				6	75.0

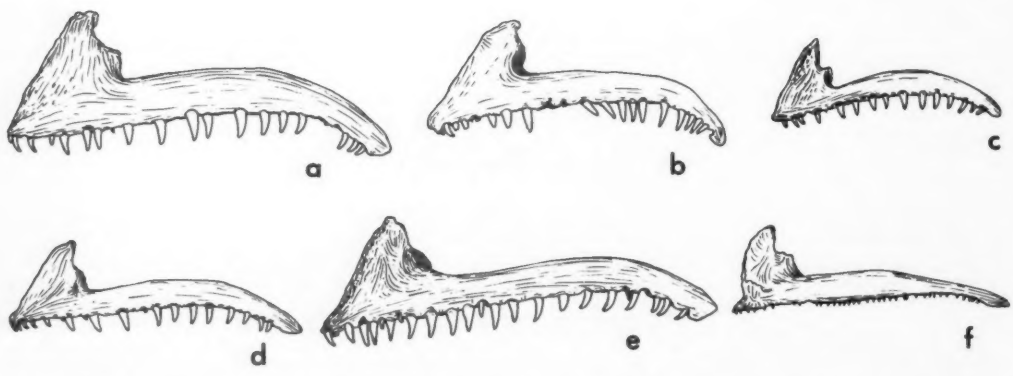


FIGURE 30.–Left premaxillae of six species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

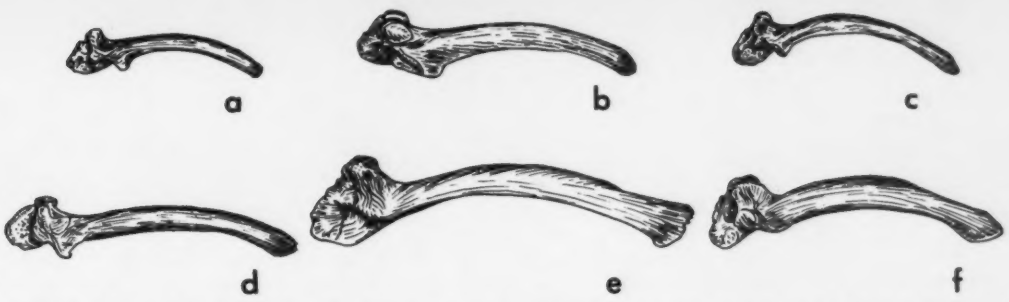


FIGURE 31.–Left maxillae of six species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

the maxillae of *Cybiosarda* and *Orcynopsis* are more pointed than in the other bonitos.

Supramaxilla.–The supramaxilla covers the posterior part of the maxilla and is partly covered anteriorly by the lachrymal (see Figure 9). It has a flat oval posterior main body and an anterior process which forms a shelf on the inner surface of the bone that continues as a ridge posteriorly. *Allothunnus* has a smoother dorsal margin and a more gradual transition between the process and the body giving the bone a more triangular shape (Figure 32h). The posterior edge of the supramaxilla of *Gymnosarda* is more curved and the anterior process is blunter (Figure 32g). *Orcynopsis* has a much deeper main body than *Cybiosarda*. Godsil (1954) used the width of this bone (called auxiliary maxillary) to separate *Sarda chiliensis* from *S. orientalis* in the eastern Pacific. He found the bone to be much narrower in relation to length in *S. orientalis* (ratio of width to length 4.1-4.4) than in northeast Pacific *S. chiliensis* (ratio 3.0-3.1). We also found that the main body of the supramaxilla is broader in *S. chiliensis* and narrower in *S. orientalis*. There do not appear to be any significant differences between northeast and southeast Pacific populations of *S. chiliensis* or between Indo-West Pacific and eastern Pacific *S. orientalis* in this character. *Sarda sarda* and *S. australis* have the supramaxilla intermediate in width between the wide bone present in *S. chiliensis* and the narrow bone in *S. orientalis*.

Dentary.–The dentary divides posteriorly into a dorsal dentigerous branch and a ventral branch, which are usually about equal in length, although the ventral branch is slightly longer in *Gymnosarda* and *Allothunnus* and sometimes in *Sarda* (Figure 33e, f). *Allothunnus* has a row of numerous (40-50) tiny teeth on the dentary while the other genera have fewer (10-25) strong conical teeth. The number of teeth varies among genera and species (Table 6). The shape of the anterior margin of the dentary can be used to divide the bonitos into three distinct groups. The anterior margin of the bone forms an acute angle with the dentigerous dorsal margin in *Sarda*, and there is a notch present at the upper portion of the anterior margin. The notch is deeper and located in the middle of the margin in *Allothunnus* (Figure 33f). *Cybiosarda*, *Orcynopsis*, and *Gymnosarda* lack an anterior notch (Figure 33a, b, e). Another notch is present in *Gymnosarda*, on the anterior part of the ventral margin; there is a slight depression in this position in the other genera of bonitos. In overall shape and size, the dentary of *Sarda* is more elongate, especially that of *S. orientalis*. The angle between the dorsal and ventral arms of the dentary is slightly greater in *Gymnosarda*. The dorsal branch is wider, flatter, and thinner in *Allothunnus*.

Angular and Retroarticular.–The triangular anterior end of the angular (frequently called articular) fits into the dentary anteriorly (Figure 9). *Allothunnus* has the most elongate angular (Figure 34f). The strongest angular is found in *Gymnosarda* (Figure 34e) followed by *Cybiosarda* and *Orcynopsis* (Figure 34a, b). An anteriorly projecting spine is present on the ventral edge of the angular. This spine is thin and weak in

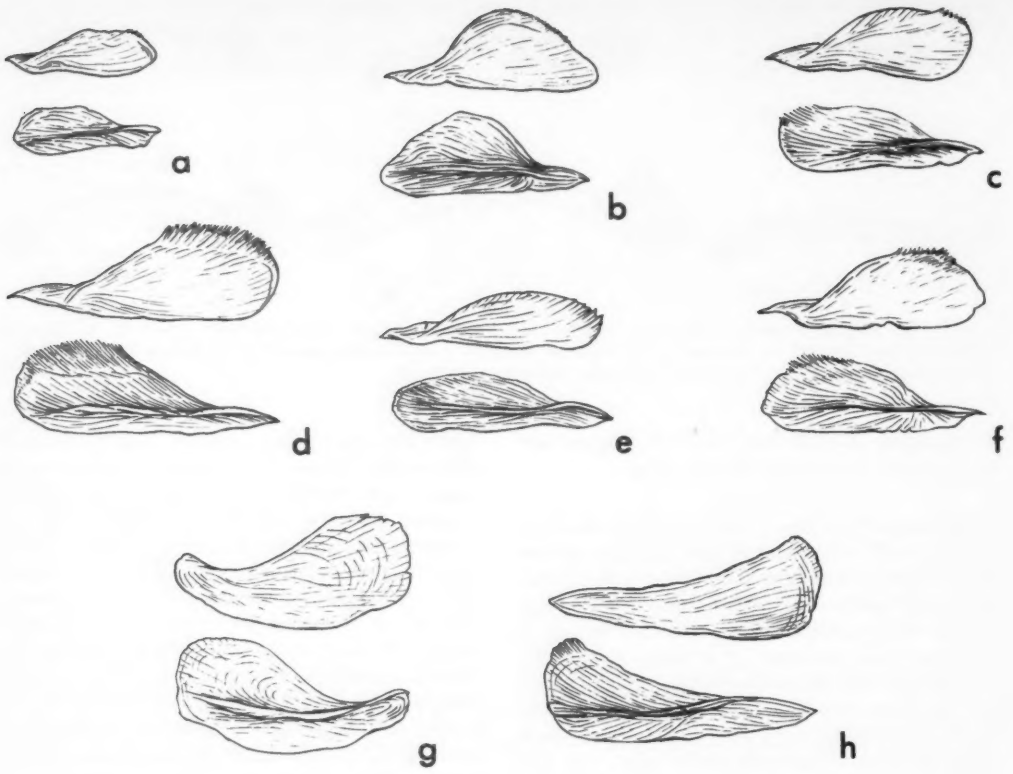
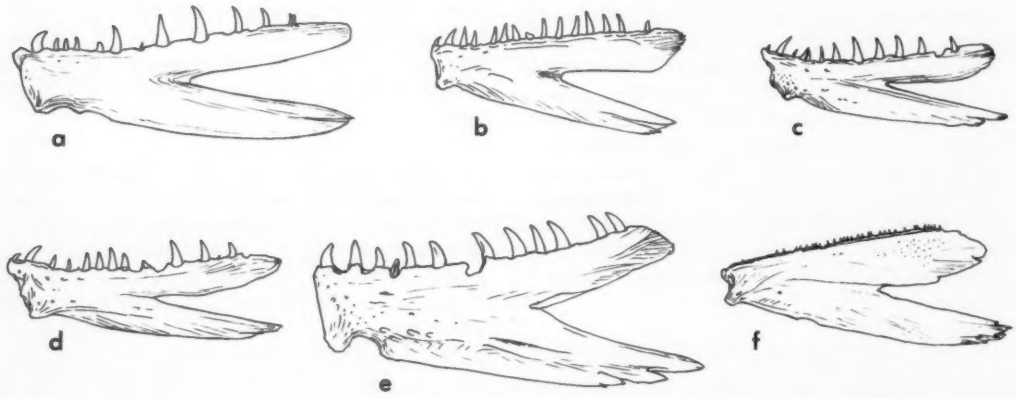


FIGURE 32.—Left supramaxillae of eight species of Sardini, upper figure of each pair is the external view, lower the internal view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 453 mm FL. d. *Sarda chiliensis*, Callao, Peru, 571 mm FL. e. *Sarda orientalis*, Jalisco, Mexico, 434 mm FL. f. *Sarda sarda*, Tunisia, 504 mm FL. g. *Gymnosarda unicolor*, Truk Islands, 787 mm FL. h. *Allothunnus fallai*, Tasmania, 775 mm FL.



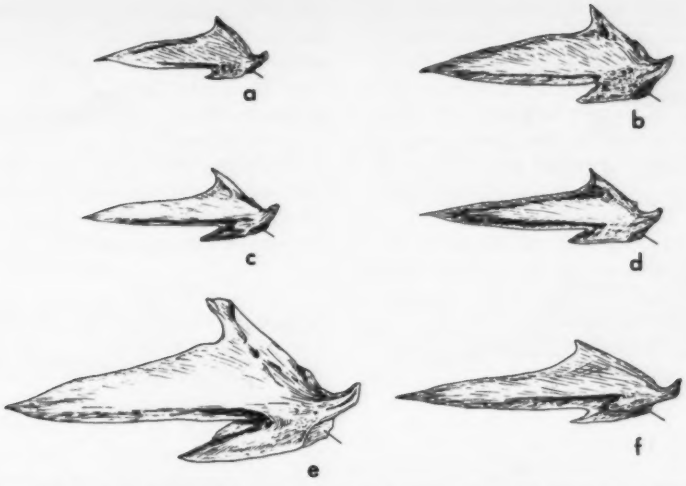


FIGURE 34.–Left angulars and retroarticulars of six species of Sardini, external view. Line indicates position of retroarticular. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

Allothunnus as in *Thunnus*. There is also an anterodorsally projecting spine on the dorsal edge of the angular. This spine has a sharp point in the bonitos, except in *Gymnosarda* where the spine is heavier and blunt as in *Scomberomorus*. The retroarticular bone (frequently called angular) is rhomboid and attached firmly to the posteroventral margin of the angular. No differences were found among the retroarticulars of the bonitos.

PALATINE ARCH.–The palatine arch consists of four pairs of bones in the roof of the mouth: palatine, ectopterygoid, entopterygoid, and metapterygoid.

Palatine.–For illustration (Figure 35), the palatine bones were placed flat with the external side up and tipped so that when viewed from above the palatine teeth and part of the anterior end of dorsal ridge were exposed. A longer ventral ridge and a shorter dorsal ridge are present as in *Thunnus*. *Cybiosarda*, *Orcynopsis*, *Gymnosarda*, and *Allothunnus* have slightly elongated dorsal ridges compared to *Sarda* (Figure 35c, d). The anterior process of the dorsal ridge is hooked in all bonitos except *Allothunnus* in which the distance between the process and the front of the ventral ridge is greater (Figure 35f).

Teeth are located along the inferior margin of the ventral ridge. Palatine teeth vary from a relatively few, large, conical teeth curved posteriorly and arranged in a single row to a broad roughened patch of tiny villiform teeth. Species of *Sarda* have one row of small conical teeth, the number of teeth varying from 7 to 22, usually 10-18. *Sarda chiliensis* has the most palatine teeth (9-22, $\bar{x}$ 15.2) but it broadly overlaps with the other three species: *S. sarda* (8-21, $\bar{x}$ 12.3), *S. orientalis* (8-19, $\bar{x}$ 11.9), and *S. australis* (7-14, $\bar{x}$ 10.7). *Cybiosarda* has about 50 small teeth in two or three rows; *Orcynopsis* about 75 tiny teeth in a patch one or two rows wide posteriorly and about five rows anteriorly; and *Gymnosarda* has an elongate oval tooth patch with hundreds of tiny teeth. There are even more and smaller teeth in *Allothunnus*, so small that Nakamura and Mori (1966) thought they were absent.

Ectopterygoid.–All bonitos have a slender T-shaped ectopterygoid (Figure 36). The ventral

FIGURE 33.–Left dentaries, external view, of six species of Sardini. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 495 mm FL. d. *Sarda orientalis*, Tokyo, 500 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 775 mm FL. f. *Allothunnus fallai*, Tasmania, 775 mm FL.

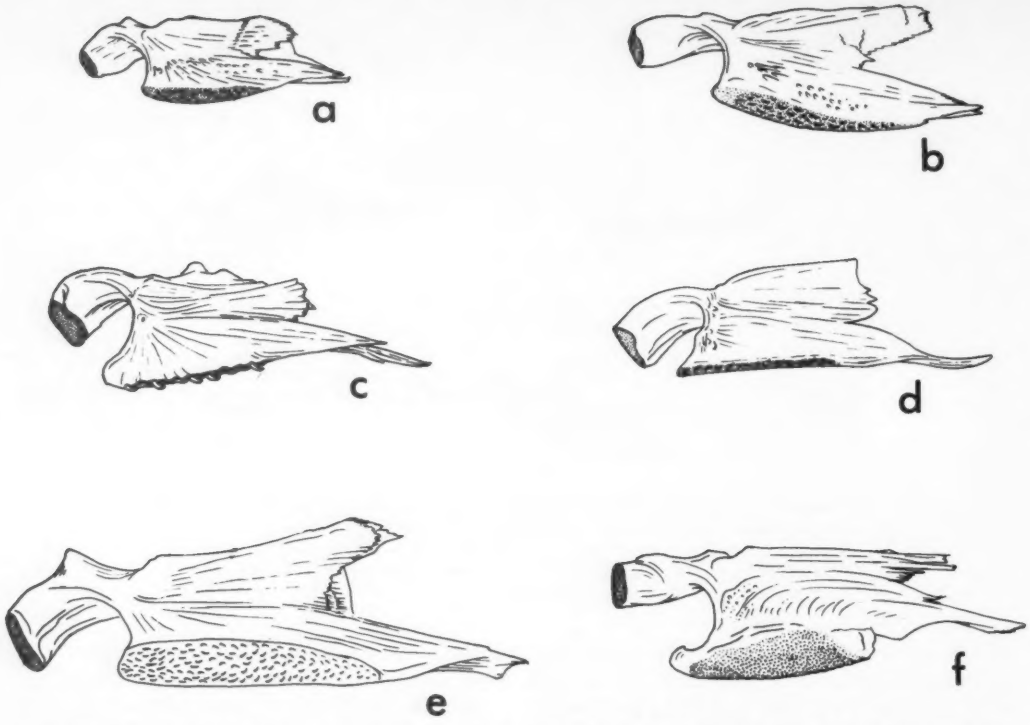


FIGURE 35.—Right palatines of six species of Sardini, internal view rotated slightly to better show palatine teeth. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda orientalis*, Tokyo, 500 mm FL. d. *Sarda chiliensis*, Callao, Peru, 549 mm FL. e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL.

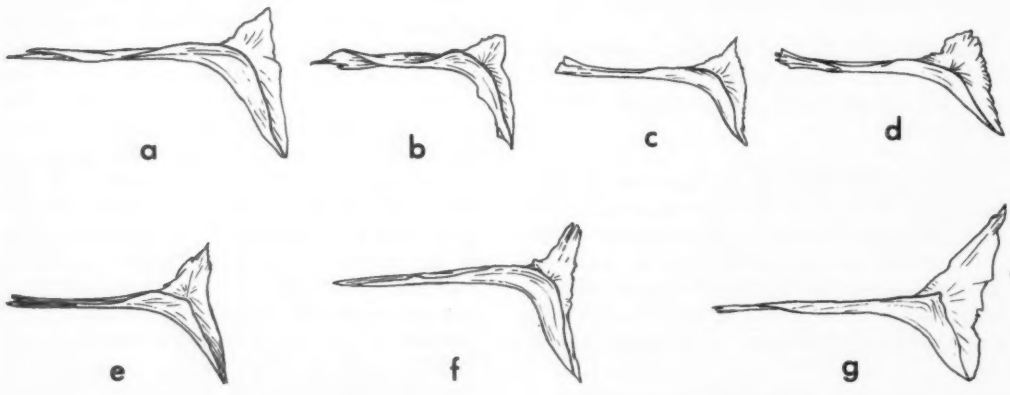


FIGURE 36.—Left ectopterygoids of seven species of Sardini, external lateral view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda sarda*, Tunisia, 504 mm FL. d. *Sarda orientalis*, Tokyo, 500 mm FL. e. *Sarda chiliensis*, Callao, Peru, 549 mm FL. f. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. g. *Allothunnus fallai*, California, 680 mm FL.

projection of the ectopterygoid is longer than the dorsal projection except in *Allothunnus* which has a larger dorsal projection. The ridge extending from the main axis to the tip of the ventral projection has a sharper angle in *Allothunnus* compared to the smooth curve in the other bonitos. The main shaft of the ectopterygoid is thicker and higher in *Gymnosarda* than in the other bonitos. *Sarda orientalis* has the dorsal projection slightly expanded instead of pointed as in the other species of *Sarda*.

Entopterygoid.–The entopterygoid is elongate oval in shape in all the bonitos (Figure 37). The external margin of the entopterygoid is the strongest and thickest part of the bone, and there is a bent posterior end which attaches to the ectopterygoid externally. *Allothunnus* has a more elongate entopterygoid and *Gymnosarda* has a broader one than the other bonitos.

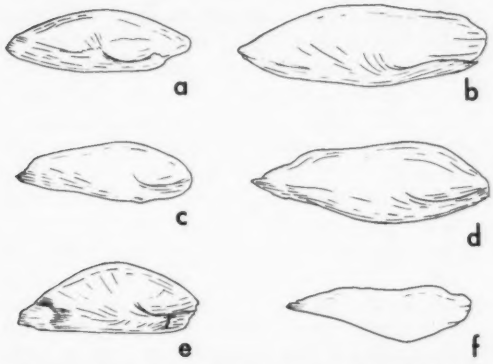


FIGURE 37.–Left entopterygoids of six species of Sardini, dorsal view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 573 mm FL. c. *Sarda australis*, New South Wales, 363 mm FL. d. *Sarda sarda*, Azores, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL. a-d drawn twice as large as e and f.

Metapterygoid.–The posterior and dorsal margins of the metapterygoid articulate with the hyomandibula (Figure 9). A groove is present on almost the entire posterior margin in all bonitos except *Allothunnus*, which has a deeper and wider groove on the upper half of the posterior margin, as in *Thunnus*. *Cybiosarda*, *Orcynopsis*, and *Sarda* have a thin projection along the upper half of the posterior margin extending from the internal surface of the metapterygoid (Figure 38). These three genera also have a posteroventral notch on the inner surface of the bone into which the anterodorsal process of the symplectic fits. The metapterygoid of *Gymnosarda* is more elongate and triangular in shape and has no projection along the posterior margin. In *Allothunnus*, the anteroventral and posteroventral margins are very similar to those in *Thunnus* (Gibbs and Collette 1967, fig. 7).

HYOID ARCH.–The hyoid arch is the chain of bones that connect the lower jaw and the opercular apparatus with the skull. The arch is composed of the hyomandibula, symplectic, quadrate, hyoid complex (basihyal, ceratohyal, epihyal, interhyal,

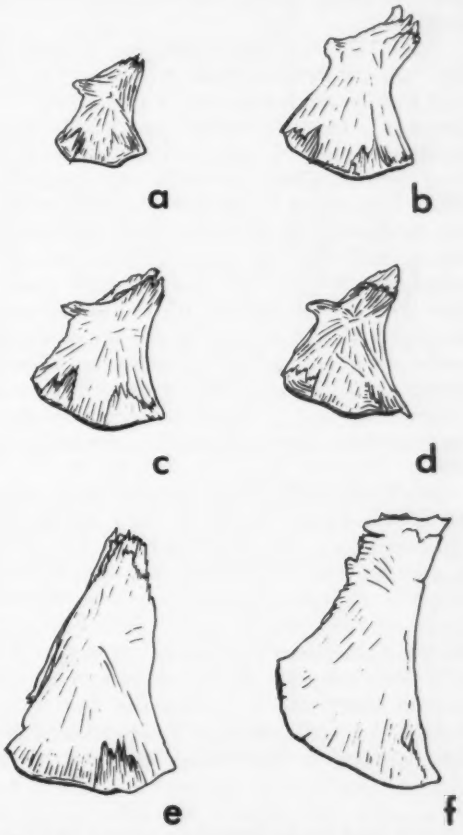


FIGURE 38.–Left metapterygoids of six species of Sardini, internal view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda orientalis*, Tokyo, 500 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL.

and the seven branchiostegal rays), and two median unpaired bones, the glossohyal and urohyal.

Hyomandibula.–The hyomandibula is an inverted L-shaped bone that connects the mandibular suspensorium and opercular bones to the neurocranium (Figure 9). Dorsally, there are three prominent condyles. The longest and anteriormost forms the base of the L and fits into the fossa at the junction of the pterotic and sphenotic bones. The dorsal condyle articulates with the ventral fossa of the pterotic and the lateral process is attached to the inside of the opercle. Anterolaterally the hyomandibula joins the metapterygoid; posterolaterally it has a long articulation with the preopercle.

Godsil (1954, 1955) found two differences between the hyomandibula in *Sarda orientalis* and *S. chiliensis*. In both species a spine protrudes posteriorly from the center condyle. The spine forms an angle of 90° or less with the major axis of the hyomandibula in *S. orientalis* and greater than 90° in *S. chiliensis*. We confirm this difference and use the character to divide the bonitos into groups. *Sarda chiliensis*, *Cybiosarda* (Figure 39a), and *Orcynopsis* (Figure 39b) have the angle greater than 90°; *Gymnosarda* and *Allothunnus* probably belong in this group based on the angle, but the spines are greatly reduced in both genera. *Sarda orientalis* has the angle 90° or less. *Sarda sarda* (Figure 39c) and *S. australis* are intermediate between the two groups in having the angle about 90°.

Godsil used the length of the spine on the ridge of bone next to the groove into which the preopercle fits as a second character to distinguish *S. orientalis* from *S. chiliensis*. The spine is much longer in *S. orientalis* and projects beyond the center condyle when the spine is placed flat with the internal side down. Again we can confirm this difference and note that *S. sarda* agrees with Godsil's description of *S. orientalis*. *Sarda australis* and *S. chiliensis* have the spine short and not protruding. Godsil (1955:34) noted that on one

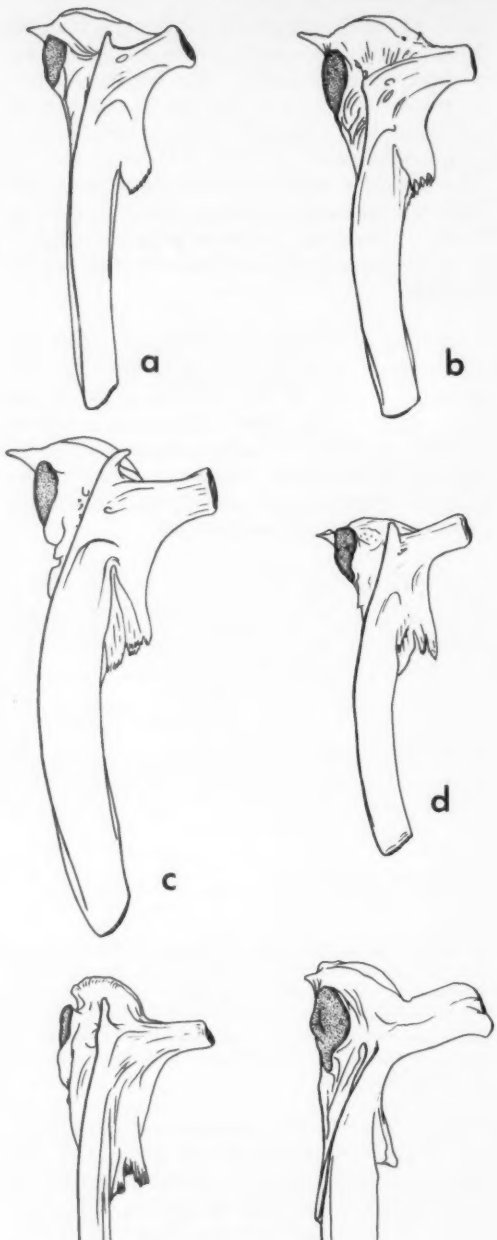


FIGURE 39.–Right hyomandibulae of six species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda sarda*, Tunisia, 504 mm FL. d. *Sarda australis*, New South Wales, 495 mm FL. e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL. a and c drawn twice as large as e and f, b and d drawn 1.5 times as large.

side of one hyomandibula of a Tokyo specimen of *S. orientalis*, the spine was short as in *S. chiliensis*. We found one specimen of *S. chiliensis* from Callao, Peru in which the spine projected as in *S. orientalis*. Thus, this difference is not absolute but "corroboratory" as Godsil has noted. *Cybiosarda* (Figure 39a) and *Gymnosarda* (Figure 39e) resemble *S. chiliensis* but the spine is still shorter. The ridge forms an angle but no spine is present in *Orcynopsis* (Figure 39b) and *Allothunnus* (Figure 39f).

The lateral condyle is broader in *Allothunnus* than in other bonitos, and its lower anterior vertical margin, where the metapterygoid attaches, does not project as far (Figure 39f). Also, the groove into which the preopercle fits is more curved in *Allothunnus*.

Symplectic.–The symplectic is a small bone that fits into a groove in the quadrate (Figure 9). Bonitos fall into three groups based on the shape of the symplectic. *Orcynopsis*, *Cybiosarda*, and *Sarda* (Figure 40a-d) have a wider upper part with a pointed or "flared" anterodorsal projection as in *Thunnus*. *Gymnosarda* has a rather thick upper part and only a slight lateral expansion about the middle of the anterior margin (Figure 40e). The anterolateral expansion of the symplectic is better developed in *Allothunnus* (Figure 40f) than in *Gymnosarda*, but there is no anterior projection at the upper end.

In external view, there is a longitudinal axis to the symplectic which is shaped differently in the three groups. *Gymnosarda* has a much thicker upper end. The upper part is also thick but somewhat flattened in *Allothunnus* as also noted by Nakamura and Mori (1966). *Orcynopsis*, *Cybiosarda*, and *Sarda* all have a notch at about the middle of the axis on the external surface of the bone which is absent in *Gymnosarda* and *Allothunnus*.

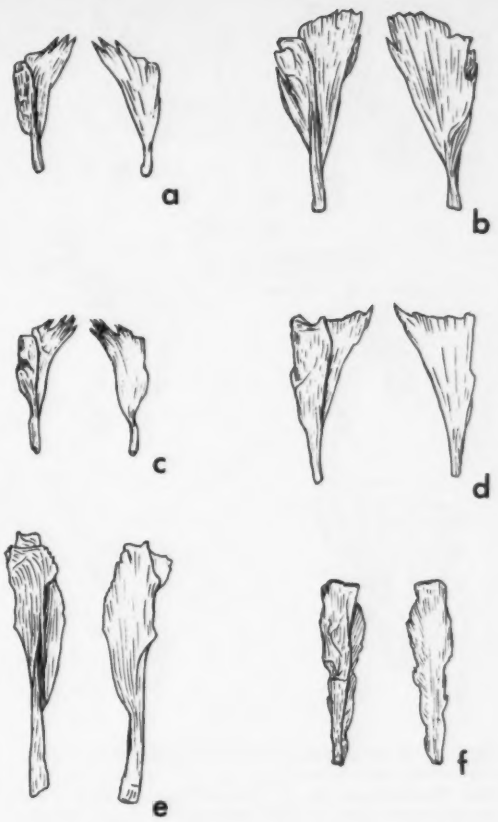


FIGURE 40.–Right symplectics of six species of Sardini, left figure of each pair is the external view, right the internal view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 573 mm FL. c. *Sarda australis*, New South Wales, 363 mm FL. d. *Sarda chiliensis*, Callao, Peru, 437 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 775 mm FL. f. *Allothunnus fallai*, Tasmania, 775 mm FL. a-e drawn twice as large as f.

Quadrate.–The lower jaw is suspended from the cranium by means of the articulating facet of the ventral surface of the triangular quadrate (Figure 9). The quadrates are similar in all bonitos, with a deep groove where the symplectic fits along the inner posterior margin and a posterodorsal process (Figure 41). The quadrate of *Allothunnus* has a distinctly longer posterodorsal process resembling those in *Thunnus*. The process in *Gymnosarda* (Figure 41e) has a slightly broader tip and also its base is expanded more than in other genera of bonitos.

Hyoid Complex.–This complex, as discussed here, includes the hypohyal, ceratohyal, epihyal, and interhyal bones and the seven branchiostegal rays (Figure 42). The external view of the four bones in *Sarda orientalis* and *Gymnosarda unicolor* has been previously illustrated by Kishinouye (1923:326) along with the hyoid arches of six other genera of Scombridae.

The hypohyal is composed of a dorsal and a ventral segment fused longitudinally along a

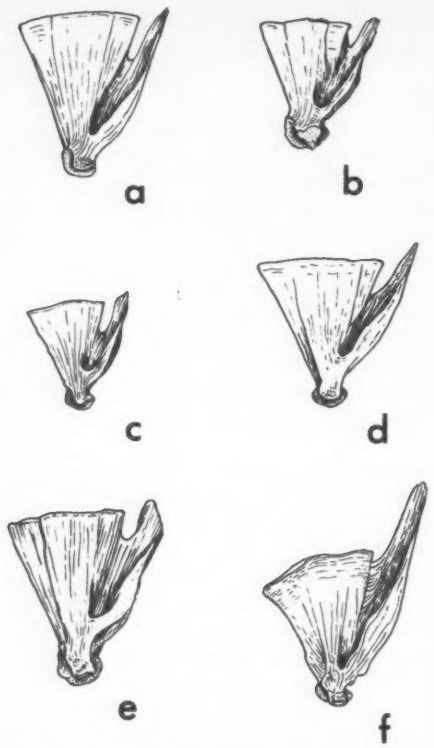


FIGURE 41.—Right quadrates of six species of Sardini, internal view to show groove for symplectic. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda sarda*, Florida, 333 mm FL. d. *Sarda australis*, New South Wales, 495 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

serrated suture that is most prominent in *Gymnosarda* (Figure 42e). There is a depression on the outer surface at the posterior half of the suture in all bonitos, as in *Thunnus*. Internally, a lateral process at the anterodorsal end forms a symphysis with the glossohyal, urohyal, basibranchial, and the process of the hypohyal from the opposite side.

The ceratohyal is a long flat bone, broader at the posterior end and with an anteroventral projection that articulates with the posteroventral notch of the hypohyal. The middle portion of the ceratohyal is concave dorsally in all bonitos. There are three notches along the ventral margin where the anterior three branchiostegal rays attach. Bonitos have no notch at the site of attachment of the fourth branchiostegal ray. All bonitos have an elliptical ceratohyal window (Nakamura and Mori 1966, fig. 6), except for *Sarda orientalis* which has only a trace of a depression at the appropriate site (Figure 42d). A deep groove extends along the upper third of the ceratohyal from the depression of the hypohyal to the middle of the epihyal in *Gymnosarda*, but there is only a slight trace of this groove in the other bonitos.

The epihyal is a triangular bone which interlocks medially with the ceratohyal. This serrated interlocking suture is limited to the inner surface of the bone in *Cybiosarda*, *Orcynopsis*, and *Sarda* (Figure 42 a-d); there are only cartilaginous connections between these two bones on the outer surface, as in *Thunnus* (de Sylva 1955, fig. 36). *Gymnosarda* and *Allothunnus* also have well-developed interlocking sutures on the outer surface (Figure 42 e, f). The epihyal bears a small condyle on its posterior end that articulates with the inner surface of the interopercle. The fifth to seventh branchiostegal rays are attached to the outer surface of the ventral margin of the epihyal. The fifth branchiostegal is at the junction of the epihyal and ceratohyal in *Gymnosarda* and is a short distance behind the junction in other bonitos.

The interhyal is a small bone with an expanded ventral end that is attached to the epihyal dorsal to the epihyal condyle. The interhyal is attached, with connective tissue, to the symphysis of the hyomandibula, quadrate, symplectic, metapterygoid, and preopercle. The interhyal also articulates above the interopercular fossa posteriorly.

Glossohyal.—The glossohyal is a spatulate bone underlying the tongue and overlying the first basibranchial bone at the anterior end of the branchial arch (see Figure 49). *Cybiosarda* and *Orcynopsis* have a pair of oval tooth patches on the dorsal surface of the glossohyal (Figure 43a, b). *Gymnosarda* also has a pair of tooth patches on the tongue, but they are on plates over the glossohyal and are not fused to the bone (Figure 43f). The ventral surface of the tooth patches of *Gymnosarda* have a deep longitudinal ridge which fits the ventral ridge of the glossohyal laterally. On the dorsal surface of the glossohyal of *Gymnosarda*, there is a prominent longitudinal ridge on which the paired tooth patches meet. The size of the tooth patches may vary from one side to the other as in the specimen of *Orcynopsis unicolor* illustrated (Figure 43b). *Sarda* lacks tooth patches (Figure

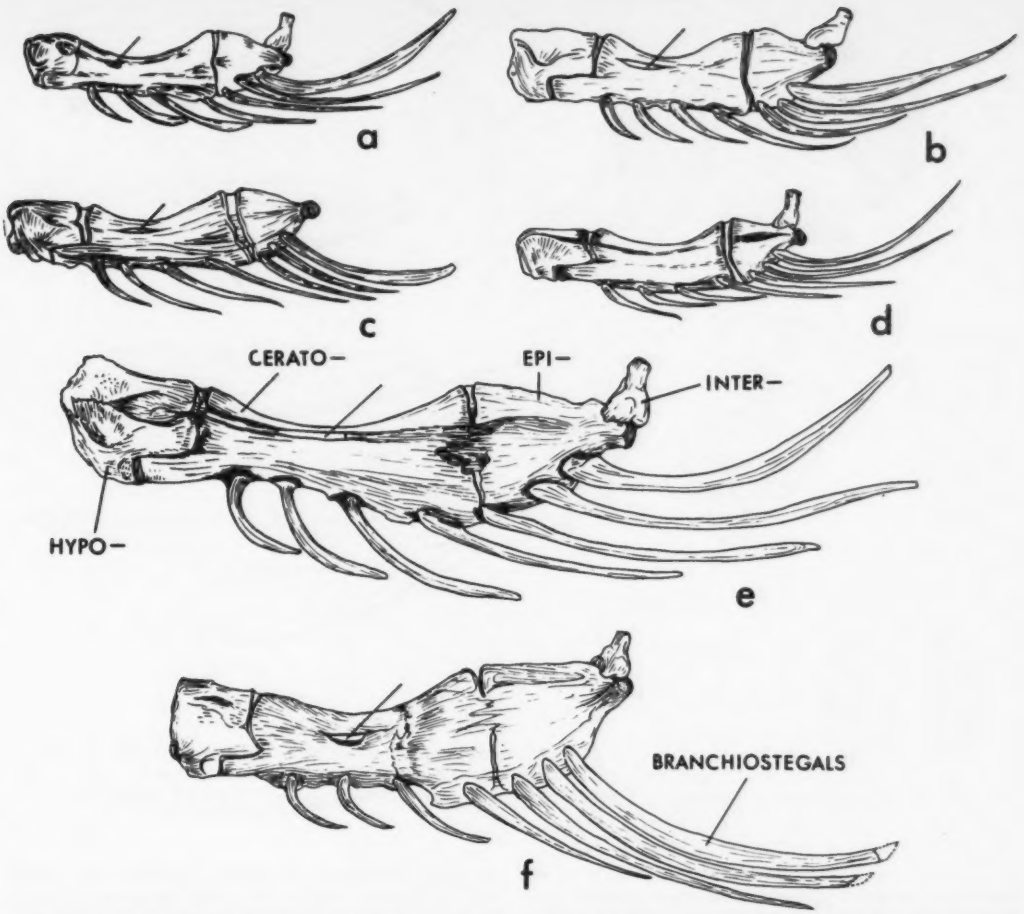


FIGURE 42.–Hyoid complex (hypohyal, ceratohyal, epihyal, and interhyal) and branchiostegal rays of six species of Sardini, external view of left side. Unlabelled line points to ceratohyal window. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 543 mm FL. c. *Sarda australis*, New South Wales, 495 mm FL. d. *Sarda orientalis*, Panama, 415 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 787 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL.

43c-e) and the shape and proportions of the glossohyal is extremely variable both inter- and intraspecifically as Godsil (1955) has pointed out for *S. chiliensis* and *S. orientalis*. A slightly concave anterior margin is present on the glossohyal of *Allothunnus*. A depression on the ventral surface of the proximal portion of the glossohyal is present in most bonitos except for *Sarda orientalis* (Godsil 1954, 1955) and *Gymnosarda*.

Urohyal.–The urohyal is a median unpaired bone. The anterior end of this element lies between, and is connected with, the hypohyals of the left and right sides. The urohyals of the bonitos have a thickened anteroventral margin which gradually narrows posteriorly (Figure 44). *Gymnosarda* has a distinctive thickened posterodorsal margin, which starts at the anterior third of the bone and forms a flattened platform at the posterior end. A similar tendency was found occasionally in other bonitos, especially *Orcynopsis*, but the thickening was limited to the middle portion of the dorsal margin. *Cybiosarda*, *Orcynopsis*, and *Gymnosarda* have relatively deep urohyals; *Sarda* and *Allothunnus* have relatively elongate urohyals.

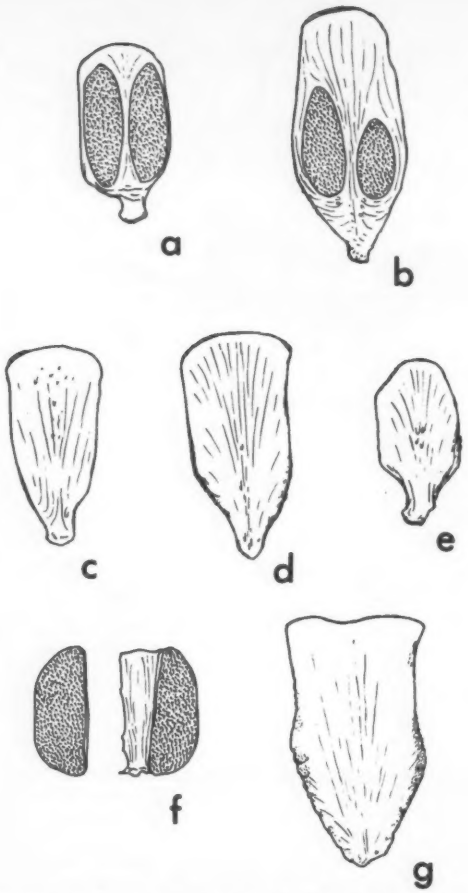


FIGURE 43.—Dorsal view of glossohyals of seven species of Sardini. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL, note unequally developed tooth patches. c. *Sarda australis*, New South Wales, 495 mm FL. d. *Sarda chiliensis*, Callao, Peru, 549 mm FL. e. *Sarda sarda*, Tunisia, 504 mm FL. f. *Gymnosarda unicolor*, Truk Islands, superficial tooth plate removed from left side of bone. g. *Allothunnus fallai*, California, 680 mm FL. a-e and g drawn twice the size of f.

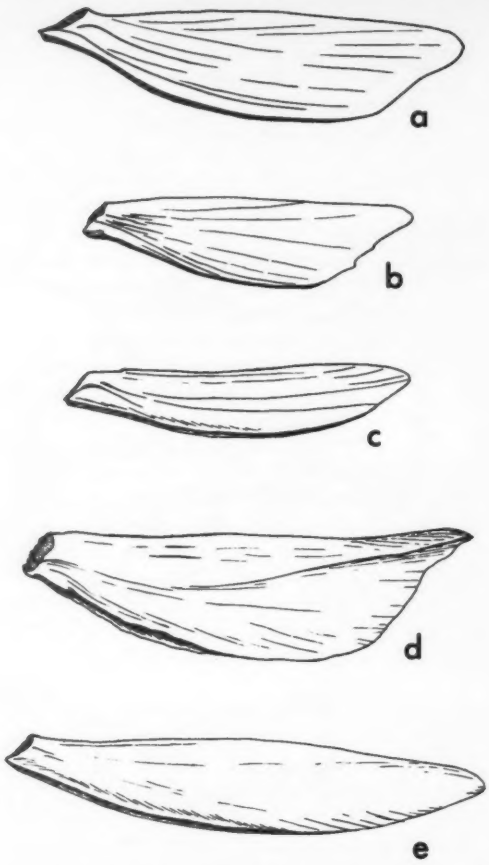


FIGURE 44.—Urohyals of five species of Sardini, in left lateral view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda chiliensis*, Callao, Peru, 549 mm FL. d. *Gymnosarda unicolor*, Truk Islands, 787 mm FL. e. *Allothunnus fallai*, California, 680 mm FL. a drawn twice as large as b-e.

OPERCULAR APPARATUS.—Four wide flat bones fit together to form the gill cover which protects the underlying gill arches.

Opercle.—The opercle is broad and more or less rectangular in shape in all bonitos except *Gymnosarda*, in which it is narrower, elongate, and more triangular (Figure 45e). *Cybiosarda*, *Orcynopsis*, and *Sarda* have similar lower posterior projections which extend beyond the posterior notch and their dorsal margins are flat or slightly concave (Figure 45a-d). *Allothunnus* has no distinct lower projection (Figure 45f).

Subopercle.—The subopercle is similar among bonitos and generally resembles those of scombrids such as *Thunnus*. *Cybiosarda*, *Orcynopsis*, and *Sarda* (Figure 46a-d) have two ridges that converge posteriorly from the anterior projection. The upper ridge articulates with the lower posterior projection of the opercle and the lower ridge connects to the posterodorsal margin of the interopercle. The ridges are much stronger

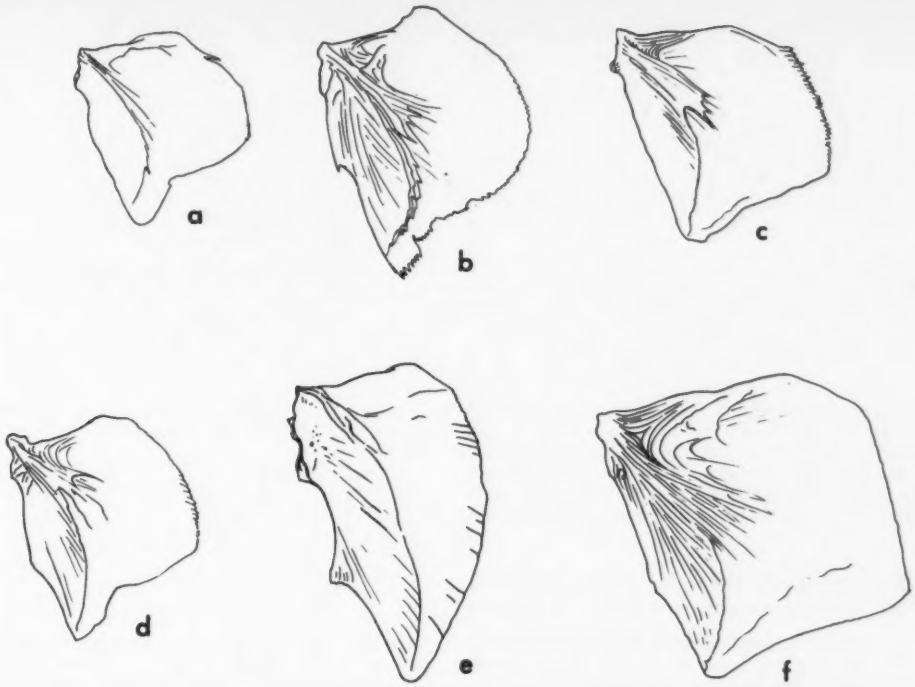


FIGURE 45.–Left opercles of six species of Sardini, external view. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda orientalis*, Tokyo, 500 mm FL. d. *Sarda australis*, New South Wales, 495 mm FL. e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

in *Cybiosarda* and *Orcynopsis* than in the species of *Sarda*. A trace of these ridges is discernible in *Allothunnus* and the bone is much thinner than in other genera. *Gymnosarda* (Figure 46e) has no ridges and the entire subopercle is more elongate than in other bonitos.

Preopercle.–The elongate preopercle is thickened along its inner surface for attachment with the hyomandibula (see Figure 9). The preopercles are similar in *Cybiosarda*, *Orcynopsis*, and the species of *Sarda* (Figure 47a-d). The dorsal projecting arm is somewhat longer and narrower in the species of *Sarda* than in *Cybiosarda* and *Orcynopsis*. As is true of the subopercle, the preopercle of *Gymnosarda* (Figure 47e) is long and narrow compared to the previous three genera. *Allothunnus* (Figure 47f) has a preopercle much more similar to *Thunnus* (de Sylva 1955:17, fig. 28) than to other bonitos. It is divided into superior and inferior arms which are approximately equal in length instead of the superior arm being longer than the inferior arm.

Interopercle.–The interopercle is roughly shaped like an elongate triangle, with a narrow anterior end. Most of the outer surface of the anterodorsal portion of the interopercle is covered by the preopercle. On the inner surface, beneath the middle of the anterodorsal margin of the interopercle, there is a condyle, which articulates with the posterior end of the epihyal and the interhyal. The anterior and posterior ends of the interopercle are narrowest in *Allothunnus* and broadest in *Gymnosarda* (Figure 48). The thinnest part of the interopercle is along the ventral margin, and a weak fimbriate posterior margin is present in all the bonitos as in *Thunnus*.

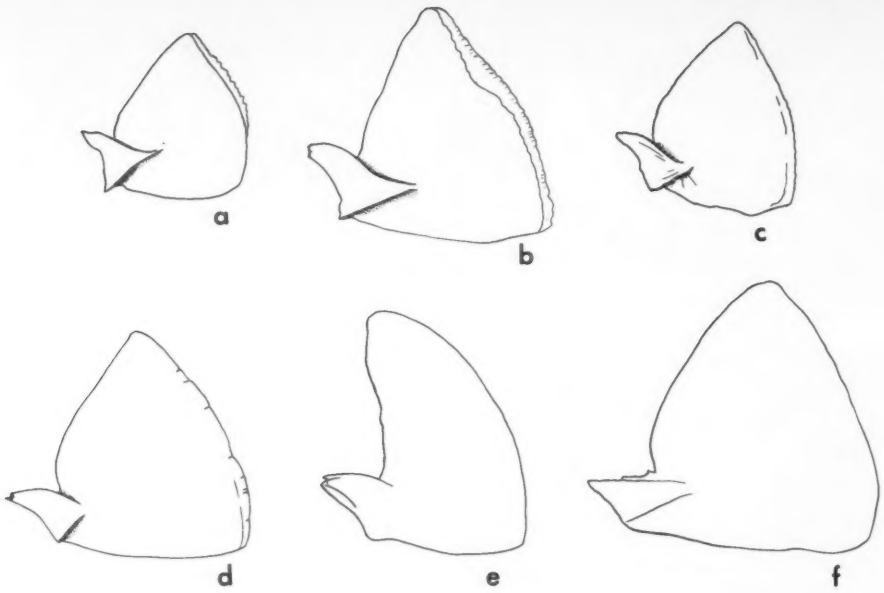


FIGURE 46.—Left subopercles of six species of Sardini, external view. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 405 mm FL. d. *Sarda chiliensis*, Callao, Peru, 549 mm FL. e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

BRANCHIAL ARCH.—The branchial arch is composed of the five pairs of gill arches: gill filaments, gill rakers, pharyngeal tooth patches, and supporting bones. The general arrangement in the Sardini (Figure 49) is similar to that found in other scombrids such as *Thunnus* (Iwai and Nakamura 1964a:22, fig. 1; de Sylva 1955:21, fig. 40), *Scomberomorus* (Mago Leccia 1958:327, pl. 12), and *Rastrelliger* (Gnanamuttu 1971:14, fig. 6). Within the Sardini, the most important generic and specific differences are in the number of gill rakers. All of the branchial bones bear patches of tiny teeth.

Basibranchials.—The three basibranchials form a chain from anterior to posterior. The first and second are about the same size and considerably shorter than the third. The first basibranchial is covered dorsally by the broad, flattened glossohyal which is dentigerous in *Cybiosarda*, *Orcynopsis*, and *Gymnosarda* as described in the hyoid arch section.

In lateral view (Figure 50), the first basibranchial has an expanded anteroventral end and is curved downward except in *Allothunnus* (Figure 50f). The second basibranchial has a prominent notch in the ventral margin that is absent in *Allothunnus*. The third basibranchial has an expanded anterior end at its junction with the second basibranchial and then tapers posteriorly. A section of cartilage extends posteriorly to articulate with the fourth ceratobranchial and lower pharyngeal.

Hypobranchials.—The first three arches have hypobranchials which connect with the ceratobranchials. The first hypobranchial is attached to the second basibranchial; the second and third hypobranchials are attached to the third basibranchial. The first two hypobranchials are longer than the third.

Ceratobranchials.—The ceratobranchials are the longest bones in the branchial arch and support most of the gill filaments and gill rakers. The first three are morphologically similar and articulate

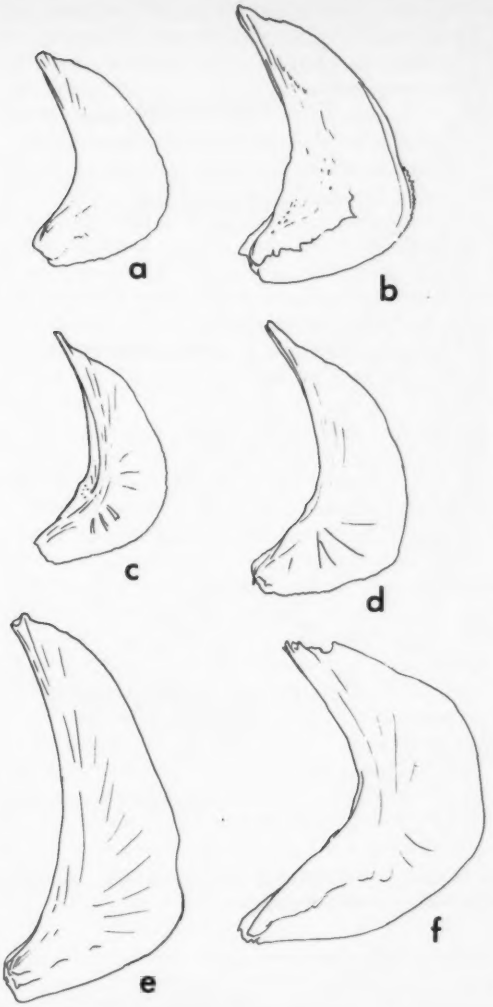


FIGURE 47.–Left preopercles of six species of Sardini, external view. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 495 mm FL. d. *Sarda chiliensis*, Callao, Peru, 517 mm FL. e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

with the posterior ends of their respective hypobranchials. The fourth is more irregular and attaches to a cartilage posterior to the third basibranchial. The fifth ceratobranchial is also attached to the cartilage, has a dermal tooth plate fused to its dorsal surface, and the complex is termed the lower pharyngeal bone. It is covered

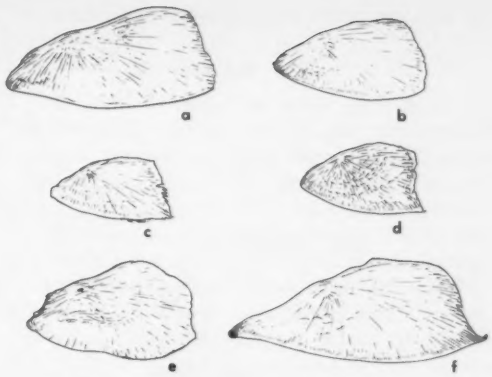


FIGURE 48.–Left interopercles of six species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 573 mm FL. c. *Sarda australis*, New South Wales, 475 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

with small conical teeth that are directed slightly posteriorly. *Allothunnus* has the smallest pharyngeal teeth among the bonitos.

Epibranchials.–The four epibranchials are attached basally to the ceratobranchial of their respective gill arch. They vary in shape with the first one being long and slender like a short ceratobranchial, the second and third shorter and stubbier, and the fourth one almost V-shaped.

Pharyngobranchials.–There are four pharyngobranchials attached basally to the epibranchial of their respective gill arch. The recurved first one articulates dorsally with the parasphenoid and is frequently referred to as the suspensory pharyngeal (Iwai and Nakamura 1964a). The triangular second pharyngobranchial bears a patch of small teeth. The third and fourth pharyngobranchials both have dermal tooth plates fused to them and are termed upper pharyngeal bones.

Gill Rakers.–The hypobranchial, ceratobranchial, and epibranchials of the first gill arch support a series of slender rigid gill rakers. The longest gill raker is at or near the junction of the upper and lower arches, between the ceratobranchial and epibranchial. Gill rakers prevent food loss through the opercular gap. There is a correlation between numbers of gill rakers, gap between gill rakers, and size of food items as

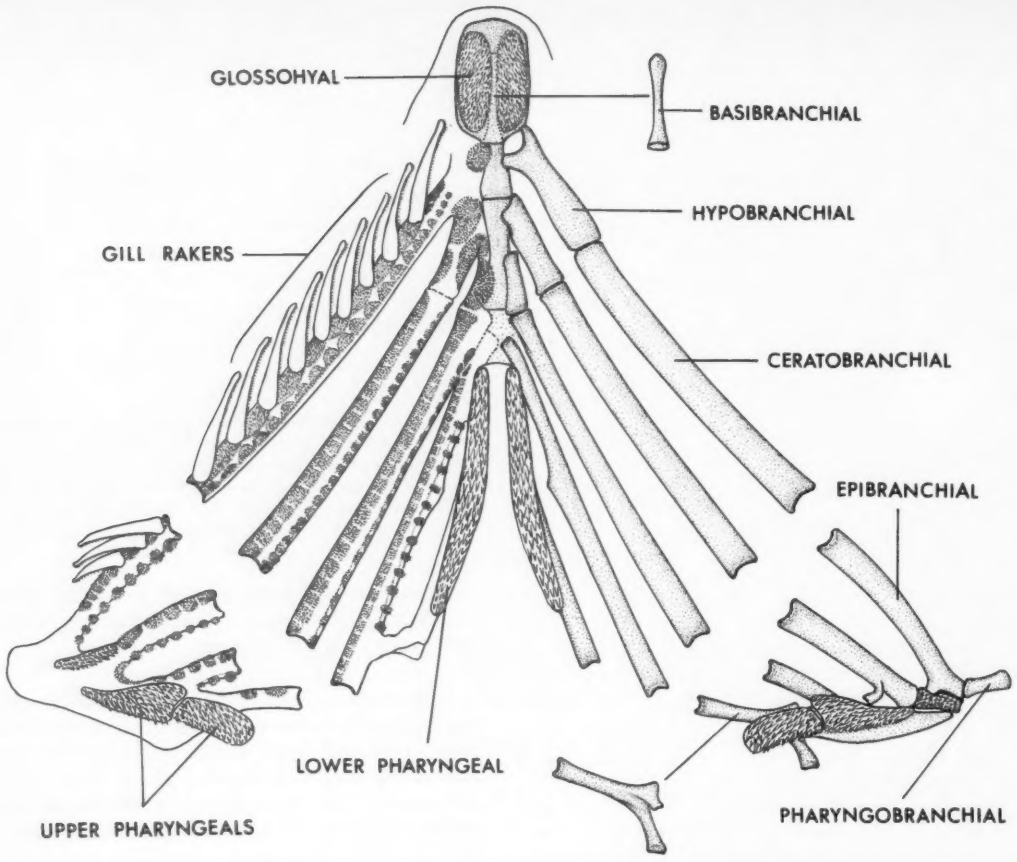


FIGURE 49.—Branchial arch of *Cybiosarda elegans*. Dorsal view of the gill arches with the dorsal halves folded back to show their ventral aspect. Epidermis removed from right hand side to reveal underlying bones.

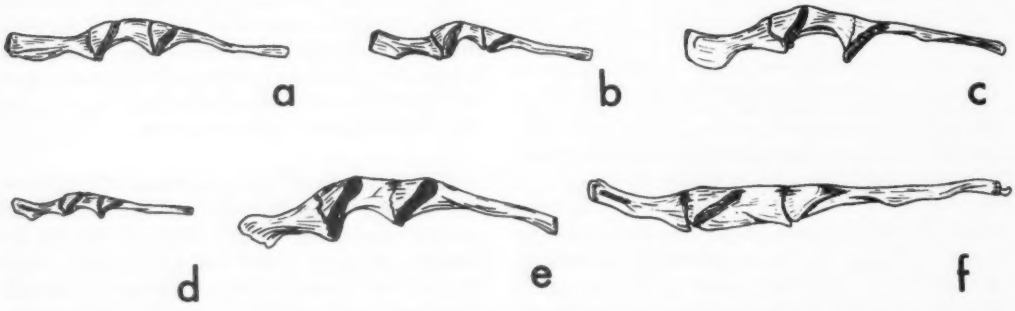


FIGURE 50.—Left lateral view of the three basibranchial bones in six species of Sardini. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 593 mm FL. c. *Sarda sarda*, Azores, 418 mm FL. d. *Sarda australis*, New South Wales, 407 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL. a-c drawn twice as large as d-f.

Magnuson and Heitz (1971) have clearly shown for a number of species of Scombridae. The number of gill rakers is easily countable and is an important taxonomic character in the Sardini as well as among other groups of the Scombridae.

Allothunnus differs strikingly from other bonitos in having many more gill rakers on the first arch, 72-80 compared to 8-27 (Table 7). The only other scombrids that approach this high number of gill rakers are *Katsuwonus pelamis* with 53-63 and two species of the genus *Rastrelliger*, *R. kanagurta* (Cuvier) and *R. brachysoma* (Bleeker), with 48-68. As discussed under dentition, the high number of gill rakers in *Allothunnus* is correlated with a high number of teeth in both upper and lower jaws.

Cybiosarda, *Orcynopsis*, and *Gymnosarda* all have few gill rakers (11-17), fewer than any other bonitos except *Sarda orientalis* (8-13).

Number of gill rakers is a valuable character within the genus *Sarda*. The largest difference is between *S. orientalis* (8-13) and *S. chiliensis* (23-27), which is particularly useful in the eastern Pacific where the tropical *S. orientalis* can be separated from *S. chiliensis* to the north and south on the basis of fewer gill rakers (and, in a similar fashion, jaw teeth). *Sarda australis*, which has been considered a subspecies of *S. chiliensis* by many authors, is intermediate in number of gill rakers (19-21) between *S. chiliensis* and *S. orientalis* but completely separated from both. There are also differences below the species level: *Sarda sarda* in the western Atlantic averages fewer (North America, 17.6; South America, 18.7) gill rakers than the other four populations, especially the Mediterranean–Black Sea (20.9) and Gulf of Guinea (20.9).

Inner Gill Rakers.–The inner surface of the hypobranchial, ceratobranchial, and epibranchial bones of the first gill arch supports a series of tubercles, the inner gill rakers. The strongest tubercle usually occurs at or near the junction of the upper and lower arches on the lower arch. The number of inner gill rakers (Table 8) is correlated with the number of gill rakers on the first gill arch (Table 7). *Allothunnus* has the longest, thickest, and most numerous inner gill rakers (49-56). In many specimens of *Cybiosarda elegans* and *Sarda orientalis* the inner gill rakers are degenerate with only a few small tubercles present. We agree with Godsil (1954, 1955) that the counts are difficult to make in *Sarda* with any consistency. Godsil used the presence of the inner gill rakers ("gill teeth") as a character to distinguish *Sarda chiliensis* from *S. orientalis* in the eastern Pacific. *Gymnosarda* completely lacks inner gill rakers, but many small conical teeth are present around the base of the gill rakers. These small teeth are also present around the base of the gill rakers in the other bonitos but they are much smaller than in *Gymnosarda*.

AXIAL SKELETON

This section is divided into six parts: vertebral number, vetebral column, infracentral grooves, ribs and intermuscular bones, caudal peduncle keels, and caudal complex.

TABLE 8.–Total number of inner gill rakers on the first gill arch in species of Sardini.

Species	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	*N*	$\bar{x}$
Cybiosarda elegans		1	1	—	—	1	—	—	—	—	2	1	—	—	1											7	10.6
Orcynopsis unicolor														2	3	2	1	3	—	2	2	—	—	—	1	16	19.8
Sarda australis											1	—	—	2	2	3	4	2	2	1	1					18	18.6
Sarda chiliensis:																											
NE Pacific														4	3	7	4	1	3	—	1					23	18.4
SE Pacific												1	1	1	2	1	2	3	2	4	1	1	1			20	19.9
Total												1	1	5	5	8	6	4	5	4	2	1	1			43	19.1
Sarda orientalis:																											
Indo-West Pacific	1	1	1	—	—	—	—	—	—	—	—	—	—	1	1											5	9.0
E Pacific		1	—	—	1	—	1	1	1	1	1	—	—	—	—	—	—	—	—	—	1					8	12.4
Total	1	2	1	—	1	—	1	1	1	1	1	—	—	1	1	—	—	—	—	—	1					13	10.8
Sarda sarda:																											
W Atlantic							3	—	3	1	4	1	9	3	—	3	2	1								30	14.3
E Atlantic											2	1	1	2	4	2	2	2	—	2						18	17.4
Total							3	—	3	1	6	2	10	5	4	5	4	3	—	2						48	15.5
Allothunnus fallai																						(49-52-54-55-56)				5	53.2

Vertebral Number

Vertebrae may be divided into precaudal (abdominal) and caudal. The first caudal vertebra is defined as the first vertebra that bears a notably elongated haemal spine and lacks pleural ribs. Vertebral counts include the ural centrum which bears the hypural plate.

As with dorsal spines, the bonitos fall into three groups based on total number of vertebrae (Table 9): few vertebrae (37-39) in *Orcynopsis*, *Gymnosarda*, and *Allothunnus*; moderate number (42-48) in *Cybiosarda* and three species of *Sarda*; and many (50-55) in *S. sarda*. These groups can be further subdivided by dividing the total count into precaudal plus caudal. *Orcynopsis* usually has 18+20=38; *Gymnosarda* 19+19=38; and *Allothunnus* 20+19=39. *Cybiosarda* has more, usually (22-23)+(24-25)=47, than the middle group of *Sarda* species, which usually have (23-25)+(20-22)=44-45. Precaudal, caudal, and total counts all vary more in *S. sarda* than in other species of bonitos.

Vertebral Column

The neural arches and spines are stout and laterally flattened on the first to fifth vertebrae in

TABLE 9.—Numbers of precaudal, caudal, and total vertebrae in species of Sardini.

Species	Precaudal vertebrae													
	17	18	19	20	21	22	23	24	25	26	27	28	*N*	$\bar{x}$
Orcynopsis unicolor	2	27											29	17.9
Cybiosarda elegans						5	6	2					13	22.8
Sarda australis							1	11					12	23.9
Sarda chiliensis:														
NE Pacific						2	34	9					45	23.2
SE Pacific						5	13	1					19	22.8
Total						7	47	10					64	23.0
Sarda orientalis:														
Indo-W Pacific							1	7	6				14	24.4
E Pacific							2	6	7				15	24.3
Total							3	13	13				29	24.3
Sarda sarda:														
W Atlantic										15	16	1	32	26.6
Mediterranean-Black Sea											11	4	15	27.3
Gulf of Guinea-S. Africa											8	9	17	27.5
Total										15	35	14	64	27.0
Gymnosarda unicolor			17										17	19.0
Allothunnus fallai				7									7	20.0

Species	Caudal vertebrae										
	19	20	21	22	23	24	25	26	27	*N*	$\bar{x}$
Orcynopsis unicolor	1	26	2							29	20.0
Cybiosarda elegans					2	5	5	1		13	24.4
Sarda australis			10	2						12	21.2
Sarda chiliensis:											
NE Pacific		1	14	26	3					44	21.7
SE Pacific			10	8	1					19	21.5
Total		1	24	34	4					63	21.7
Sarda orientalis:											
Indo-W Pacific		9	4	1						14	20.4
E Pacific		8	4	2						14	20.6
Total		17	8	3						28	20.5
Sarda sarda:											
W. Atlantic					2	13	16	1		32	24.5
Mediterranean-Black Sea							3	9	3	15	26.0
Gulf of Guinea-S. Africa							11	6		17	25.4
Total					2	13	30	16	3	64	25.1
Gymnosarda unicolor	17									17	19.0
Allothunnus fallai	7									7	19.0

TABLE 9.—CONTINUED.

Species	Total vertebrae																			N	$\bar{x}$
	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55		
Orcynopsis unicolor	3	24	3																	30	38.0
Cybiosarda elegans											11	2								13	47.2
Sarda australis									11	1										12	45.1
Sarda chiliensis:																					
NE Pacific							1	8	34	4										47	44.9
(Kuo 1970)							(1	14	54	4)										(73)	(44.8)
SE Pacific							1	17	4	1										23	44.2
(Kuo 1970)						(9	29	23	4	1)										(66)	(43.4)
Total							2	25	38	5										70	44.7
Sarda orientalis:																					
Indo-W Pacific								2	12											14	44.9
E Pacific								1	14											15	44.9
Total								3	26											29	44.9
Sarda sarda:																					
W Atlantic														4	25	4	1			34	51.1
NE Atlantic															3					3	51.0
Mediterranean-Black Sea																	11	4		15	53.3
(Demir 1964, Turkey)																(6	71	34	1)	(112)	(53.3)
Gulf of Guinea-S. Africa																2	14	—	1	17	53.0
Total														4	28	6	26	4	1	69	52.0
Gymnosarda unicolor		17																		17	38.0
Allothunnus fallai			7																	7	39.0

all bonitos except *S. sarda* (first to seventh). Posteriorly, towards the caudal peduncular vertebrae and caudal complex, the neural spines bend abruptly backward and cover most of the neural groove; caudally they merge into the caudal complex as in *Thunnus* (Kishinouye 1923; Gibbs and Collette 1967). Neurapophyses are present on all centra. The neural prezygapophyses on the first vertebra are modified to articulate with the exoccipital where the vertebral axis is firmly articulated with the skull. They are stronger at the anterior portion of the vertebrae and are spurlike spines on the peduncular vertebrae and in the caudal complex. Neural postzygapophyses arise posterodorsally from the centrum and overlap with prezygapophyses posteriorly. The postzygapophyses progressively merge into the neural spine in the peduncular region. The basic structure and elements of the neural arches and neurapophyses are similar in bonitos (Figures 51-53) to those of other scombrids (Kishinouye

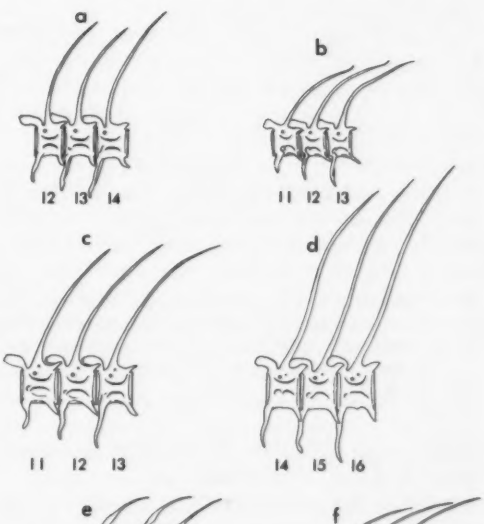


FIGURE 51.—Left lateral view of vertebra bearing first closed haemal arch (middle vertebra of each set of three) in six species of Sardini. Vertebrae numbered from anterior. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Israel, 545 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL (lumps on neural spines are anomalies). f. *Allothunnus fallai*, California, 680 mm FL.

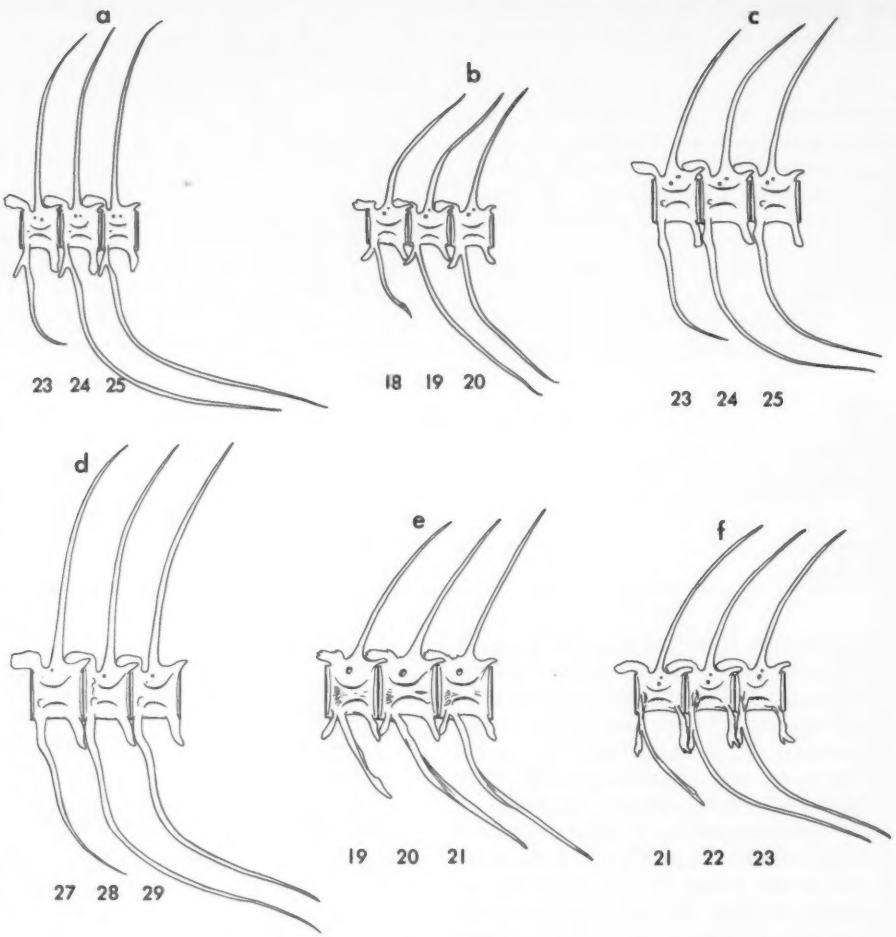


FIGURE 52.—Junction of precaudal and caudal vertebrae (middle vertebra of each set of three is first caudal vertebra) in six species of Sardini, left lateral view. Vertebrae numbered from anterior. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Israel, 545 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

1923; Conrad 1938; Mago Leccia 1958; Nakamura 1965; Gibbs and Collette 1967).

Variable characters are found on the haemal arches and haemapophyses in bonitos. Laterally directed parapophyses, arising from the middle of the centrum, appear distinctively on the third to fifth vertebrae, where the intermuscular bones and pleural ribs are encountered (see section on ribs and intermuscular bones). The parapophyses become broader and longer posteriorly and gradually shift to the anteroventral portion of the centra. In lateral view, the first ventrally visible parapophyses are found on the 8th to 10th vertebrae as described by Godsil (1954) for eastern Pacific *Sarda chiliensis* and *S. orientalis*. Posteriorly, the distal ends of the paired parapophyses meet on the 11th to 15th vertebrae forming the first closed haemal arch as Godsil (1954) found in eastern Pacific *S. chiliensis*. Nakamura (1965) suggested that the location of the first closed haemal arch can be used to assess relationships within the Thunnini. In the bonitos,

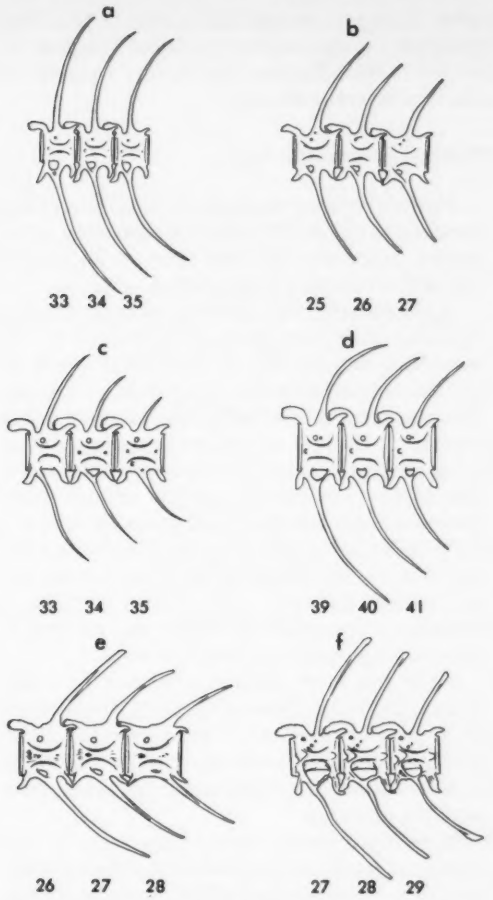


FIGURE 53.—Inferior foramina on caudal vertebrae in six species of Sardini, left lateral view. Vertebrae numbered from anterior. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Israel, 545 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

the first closed haemal arch is at the 11th to 13th vertebra in *Orcynopsis*, 13th in *Cybiosarda*, 13th to 15th in *Sarda sarda*, 12th to 14th in the other species of *Sarda*, 11th in *Gymnosarda*, and 12th in *Allothunnus*. This position is correlated with the number of vertebrae (Table 9). The first closed haemal arch is pointed anteriorly or posteriorly (Figure 51). The haemal spines become elongate and point posteriorly until they abruptly elongate on the first caudal vertebra. The paired pleural ribs (see section on ribs and intermuscular bones) attach to the distal end of the parapophyses and arches and extend posteriorly to the last precaudal vertebra. Symmetrically with the neural arches and spines on the caudal vertebrae, the haemal arches and spines bend posteriorly at the caudal peduncle and then merge into the caudal complex.

Haemapophyses include pre- and postzygapophyses but their relative positions are different from those of the neurapophyses, and they do not overlap in the bonitos. Haemal arches and haemapophyses are best developed in *Allothunnus*. The first haemal postzygapophyses arise posteroventrally from the eighth or ninth centrum, and they reach their maximum length at about the junction of the precaudal and caudal vertebrae (Figure 52). They begin at the fourth vertebra in *Thunnus* (Gibbs and Collette 1967) and the eighth vertebra in *Scomberomorus* and *Acanthocybium* (Mago Leccia 1958; Conrad 1938). The haemal postzygapophyses fuse with the haemal spine in the caudal peduncle region. The haemal prezygapophyses arise from the anterior base of the haemal arches on the 14th to 23rd vertebra, depending on the species. They begin at the 12th to 18th vertebra in "Thunninae" (Nakamura 1965; Gibbs and Collette 1967; Potthoff 1974) and at the 16th in *Acanthocybium* (Conrad 1938). As do their counterpart neural prezygapophyses, the haemal prezygapophyses persist symmetrically into the caudal complex.

The relative position and contacts between pre- and postzygapophyses of both neuro- and haemapophyses, especially the latter, vary in different regions of the vertebral column (Figures 51-53). Godsil (1954) compared haemal pre- and postzygapophyses of eastern Pacific *Sarda chiliensis* and *S. orientalis*. We believe that comparisons should be made within specific regions of the vertebral column. The haemal postzygapophysis of the last precaudal vertebra and the haemal prezygapophysis of the first caudal vertebra (Figure 52) abut each other in *Orcynopsis*, *Sarda orientalis*, and *Allothunnus*. A space between these two elements is present in other bonitos. The haemal prezygapophysis is longer than the postzygapophysis at the junction (Figure 52) of precaudal and caudal vertebrae in *Cybiosarda*, *Orcynopsis*, *S. chiliensis*, and *S. orientalis*. The opposite condition is found in *S. sarda*, *S. australis*, and *Allothunnus*.

Struts between the haemal arch and the centrum form the inferior foramina. These are variably developed on 3 to 12 vertebrae anterior to the

caudal peduncle, depending on the species (Figure 53). *Cybiosarda* has the most inferior foramina, on 10 to 12 vertebrae; *Orcynopsis* has 9 to 10; *Sarda* 3 to 7; and *Gymnosarda* 6 to 7. *Allothunnus* has the largest inferior foramina on 7 to 9 vertebrae.

Infracentral Grooves

Nakamura and Kikawa (1966) described three types of infracentral grooves on the ventral side of the vertebral centra in tunas. They placed *Sarda orientalis* in type C, with a single groove, and this is the category of all species of *Sarda*, *Cybiosarda*, and *Orcynopsis* (Figure 54). *Gymnosarda* (Figure 54e) has the type C infracentral grooves on the centra, but the grooves are much deeper and a shallow transverse septum is present in the middle of each groove. Nakamura and Kikawa (1966) did not place *Allothunnus* in any of the three categories. The precaudal vertebrae of *Allothunnus* have type A, with two separate infracentral grooves per centrum, but these are not distinct posteriorly as shown in Figure 54f. Some of the grooves may be covered with a layer of thin bone, especially on the anterior precaudal vertebrae. In all the bonitos, the grooves are very irregular on the first several vertebrae.

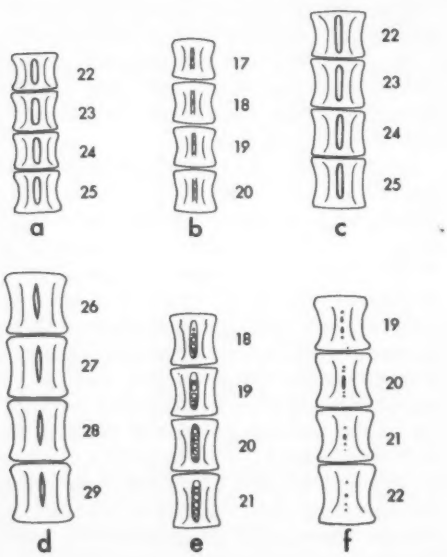


FIGURE 54.—Infracentral grooves on the ventral surface of four vertebrae including the last precaudal and first caudal vertebra in six species of Sardini. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Israel, 545 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, Tasmania, 775 mm FL. a, c, and d drawn twice as large as b, e, and f.

Ribs and Intermuscular Bones

Pleural ribs are present from the third vertebra posterior to the 18-27th vertebra, depending on the species. Intermuscular bones start on the back of the skull and extend to the 19-39th vertebra.

Sarda differs from other bonitos in having two cephalic intermuscular bones attached to the exoccipital on each side of the skull (Figures 12, 26). One is attached to the center of the exoccipital. The other one is attached to the exoccipital just anterior to the first neural prezygapophysis close to the midline of the skull. *Orcynopsis*, *Cybiosarda*, and *Allothunnus* have the median cephalic intermuscular bone, but the lateral one is represented only by an unossified ligament. *Gymnosarda* completely lacks cephalic intermuscular bones and also lacks a ligament in the lateral position. A ligament is present in the comparable position of the median cephalic intermuscular bone.

Sarda has more pleural ribs than do other genera, 19-24 pair; *Cybiosarda* has 20, *Allothunnus* 18, *Gymnosarda* 17, and *Orcynopsis* 16. These numbers are well correlated with vertebral number except that *Cybiosarda* has fewer than would be predicted.

The same general trend is apparent in the number of intermuscular bones but several genera are not in corresponding order. *Sarda sarda* has the most (36-45 pair) followed by other species of the genus (32-36). Following are *Allothunnus* (28-29) and *Gymnosarda* (25-28) with more than expected; *Cybiosarda* (23-24) with fewer than expected; and *Orcynopsis* (19-20) with the fewest.

Caudal Peduncle Keels

We believe that there is a general evolutionary trend within the Scombridae in the relative development of keels on the caudal peduncle. The Gasterochismatinae and the primitive members of the Scombrinae (Scombrini—mackerels and Scomberomorini—Spanish mackerels) lack supporting bony keels and have only external fleshy keels on the caudal peduncle. Starting with the bonitos, bony keels are developed under the largest pair of fleshy keels to strengthen and support them. They are developed in two different ways in

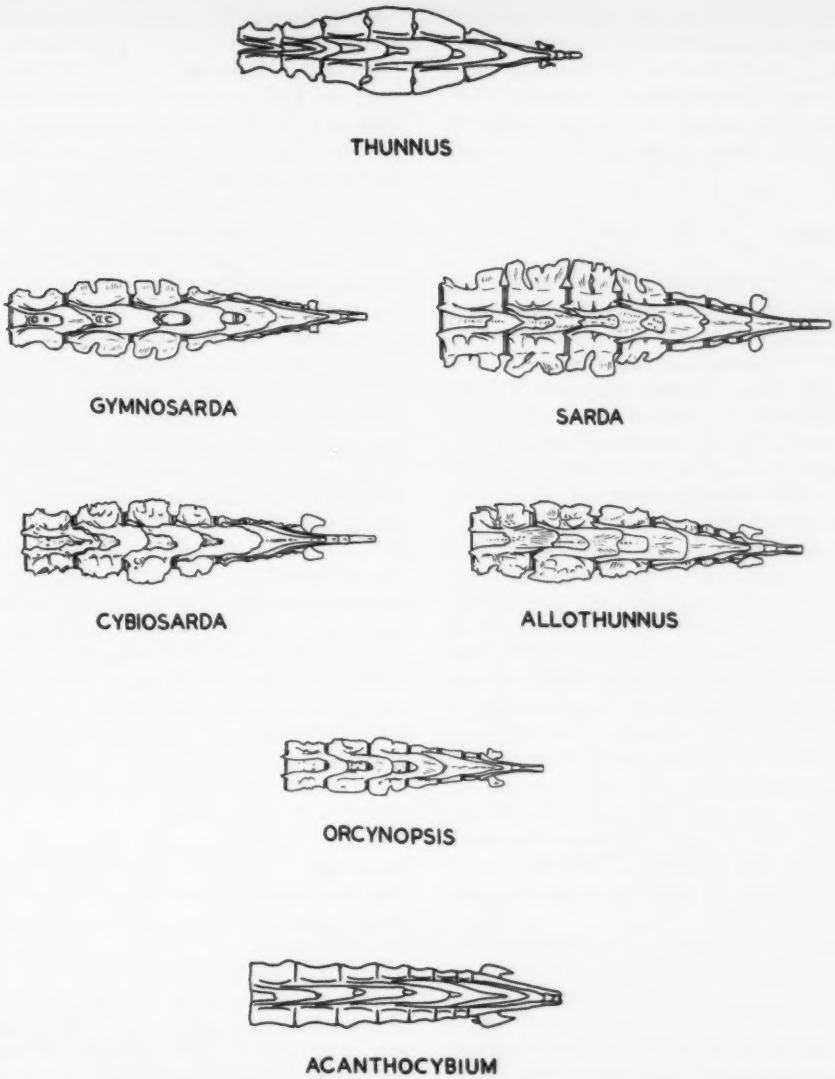


FIGURE 55.–Dorsal view of last seven or eight preural centra to show structure of bony caudal keels in the five genera of Sardini plus *Acanthocybium* and *Thunnus* representing a more primitive (Scomberomorini) and a more advanced tribe (Thunnini) respectively.

the bonitos. *Orcynopsis*, *Cybiosarda* (Figure 55), and *Allothunnus* have low keels running the entire length of the vertebrae involved. *Sarda* and *Gymnosarda* have wider keels, as in the higher tunas, but they are divided into two segments on each vertebra, one on the anterior part of the vertebra and one on the posterior part. The higher tunas (Thunnini–*Auxis* through *Thunnus*) have a wide flattened plate that acts as a single functional unit over several vertebrae.

Within the bonitos, there are minor differences as to which vertebrae bear the bony caudal keel. Counting anteriorly from preural centrum one, *Orcynopsis* differs from *Cybiosarda* in having keels concentrated on the fourth to sixth preural vertebrae instead of on the fifth to seventh.

Allothunnus has keels on the fourth to seventh; *Gymnosarda*, *Sarda australis*, *S. orientalis*, and *S. chiliensis* all have them on the four vertebrae between the fourth and eighth. Correlated with its greatly increased number of vertebrae (Table 9), *Sarda sarda* has keels on the 5th to 10th preural vertebrae.

Caudal Complex

Posterior to the peduncular vertebrae, the supporting bones of the caudal fin (Figure 56) consist of four preural centra. Preural centra four and three bear stout haemal and neural spines. Preural centrum two has a haemal spine and a fused epural. The urostyle represents a fusion of preural centrum one and the ural centrum (Potthoff 1975). The urostyle is fused with a triangular plate posteriorly and with the uroneural anteriorly. Dorsally, the urostyle bears an autogenous epural and ventrally, the autogenous parhypural. Preural centra two to four are compressed in all bonitos, as in *Thunnus*. Usually, two neural and three haemal spines bend abruptly away from the vertebral axis on these preural centra and parallel the dorsal and ventral edges of the hypural plate. Exceptions are found in some specimens of *S. sarda* and *S. chiliensis* (Figure 56c), which have an additional pair of neural and haemal spines from preural centrum five supporting caudal rays. The figure of *S. sarda* presented by Monod (1968, fig. 749) has two haemal spines on preural centrum three which is an anomaly. Other elements of the preural centra are described in the sections on the vertebral column and caudal peduncle keels.

The triangular hypural plate is composed of five fused hypural bones (Potthoff 1975). The dorsalmost (hypural 5) is not completely fused with the hypural plate in the bonitos (Figure 56c) or in the higher tunas, *Auxis* to *Thunnus*. The primitive hypural notch is absent from the middle of the posterior margin in all bonitos except for a vestige in *Gymnosarda*. The anterior epural (epural one) resembles the neural spine of the adjacent preural centrum three because it is secondarily fused to the neural arch of the second preural centrum. The posterior epural (epural two) is a free splint located between the anterodorsal margin of the hypural plate and the anterior epural in the Sardini (Figure 56b). It is absent (or may be secondarily fused to the anterior epural) in one Tunisian specimen of *S. sarda* (Figure 56d), which is an anomaly.

The parhypural has a strong hooked process, the parhypurapophysis, at its proximal end. As in *Thunnus*, it is located between the first haemal spine and the anteroventral margin of the hypural plate in all bonitos, except *Gymnosarda*. In *Gymnosarda* (Figure 56e), the parhypural is fused with the hypural plate as in *Acanthocybium* and some species of *Scomberomorus*. Kishinouye's (1923) figures of *Gymnosarda* (fig. 38) and *Acanthocybium* (fig. 39) are similar to our observations, but the caudal complex is upside down in his figure of *Gymnosarda*. Fusion of the parhypural with the hypural plate in *Acanthocybium* was also noted by Conrad (1938) and Fierstine and Walters (1968). In *Scomberomorus niphonius*, we also find this fusion, which is in agreement with Kishinouye's (1923) fig. 41. However, the parhypural is not fused with the hypural plate in *Scomberomorus chinense* (Kishinouye 1923, fig. 40) and the three western Atlantic species of *Scomberomorus* described by Mago Leccia (1958). The shape of the parhypurapophysis separates *Cybiosarda*, *Orcynopsis*, and *Gymnosarda* from *Sarda* and *Allothunnus*. The former have a smooth oblique anterior margin and the latter are concave. The concentrations of tendons and muscular bands between the parhypurapophysis and caudal rays in scombroids were described by Fierstine and Walters (1968), but no specific study of this aspect was made during our work.

One of the diagnostic characters of the Scombridae is that the bases of the caudal rays cover the hypural plate (Figure 57), instead of only extending part way over the plate as is true of the Gempylidae and Trichiuridae. Another diagnostic character of the Scombridae is that four preural centra support the caudal rays (Figure 57). In the Gempylidae, Carangidae, and Coryphaenidae, only three preural centra support the caudal fin rays (Berry 1969; Potthoff 1975).

DORSAL AND ANAL FINS

Scombrids have two dorsal fins. The first dorsal fin is composed of stiff spines and is separated from the second dorsal by a short distance, except in *Rastrelliger*, *Scomber*, and *Auxis* which have a greater distance between the fins. The second dorsal fin is composed of soft rays and is followed by a series of free finlets, 6-10 in the Sardini. The anal fin is located approximately opposite the dorsal fin and is composed largely of soft rays

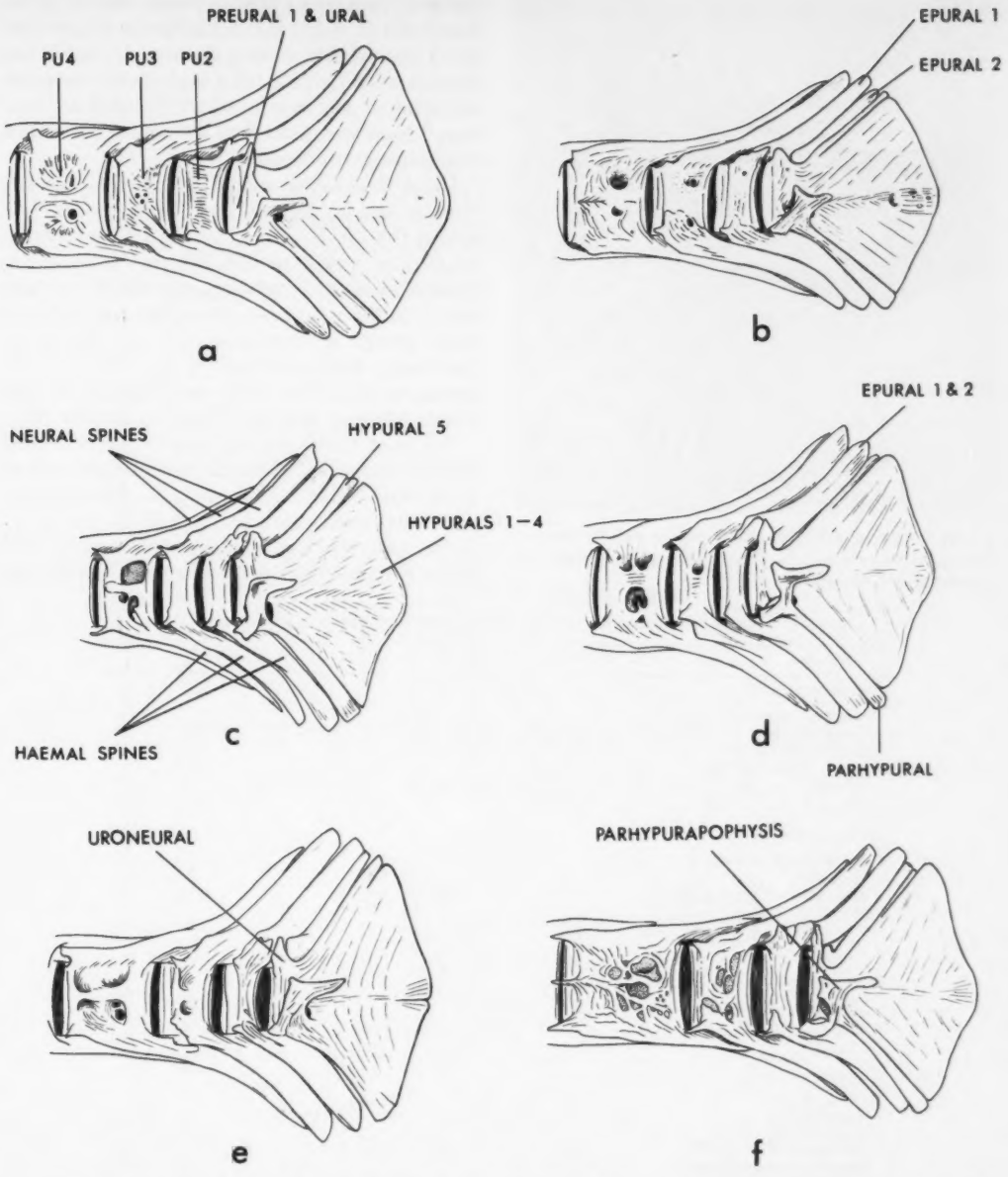


FIGURE 56.—Left lateral view of caudal complex of six species of Sardini. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 573 mm FL. c. *Sarda chiliensis*, Callao, Peru, 571 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL (with anomalous fusion of the two epurals). e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, California, 680 mm FL. a is drawn twice as large as b, e, and f, and c and d are 1.5 times as large as b, e, and f.

FIGURE 57.—Radiograph of the caudal complex with the bases of the caudal fin rays covering the hypural plate. *Orcynopsis unicolor*, Dakar, 960 mm FL.

followed by a series of anal finlets similar to the dorsal finlets. Some scombrids have a free or partially free spine preceding the anal fin, but in the Sardini it is difficult to tell if the anterior elements are spiny or soft rays so all are included as "anal rays." Numbers of fin rays are useful taxonomic characters in the Sardini.

Using the number of dorsal spines (Table 10), bonitos can be divided into three groups: few spines (12-15) in *Orcynopsis* and *Gymnosarda*; moderate numbers (16-19) in *Cybiosarda*, *Allothunnus*, and three species of *Sarda*; and many (20-23) in *S. sarda*. The difference between these groups is correlated with the number of vertebrae. Intraspecifically, eastern Atlantic specimens of *Sarda sarda* have modally higher counts (22) than western Atlantic specimens (21).

The most distinctive bonito in counts of second dorsal elements is *Cybiosarda*, with a high count of 17-19 rays (Table 11). *Orcynopsis*, *Gymnosarda*, and *Allothunnus* have low counts (15 or fewer). *Sarda australis* has, modally, one more second dorsal ray than do *S. orientalis* and *S. chiliensis*.

TABLE 10.—Number of spines in the first dorsal fin of species of Sardini.

Species	11	12	13	14	15	16	17	18	19	20	21	22	23	*N*	$\bar{x}$
Cybiosarda elegans						12	9	1						22	16.5
Orcynopsis unicolor:															
E Mediterranean		1	28	7										36	13.2
Cent. Mediterranean			10											10	13.0
(Postel 1956a, Tunisia)	(3	22	161	3)										(189)	(12.9)
Atlantic			4	2										6	13.3
Total		1	42	9										52	13.2
Sarda australis								7	12					19	18.0
Sarda chiliensis:															
NE Pacific								19	16					35	18.5
(Kuo 1970)							(20	420	69	2)				(511)	(18.1)
SE Pacific							5	19	7					31	18.1
(Kuo 1970)							(8	77	5)					(90)	(18.0)
Total							5	38	23					66	18.3
Sarda orientalis:															
Indian Ocean								10						10	18.0
NW Pacific								11	4					15	18.3
Cent. Pacific								2	2					4	18.5
E Pacific							4	11	1					16	17.8
Total							4	34	7					45	18.1
Sarda sarda:															
North America										6	46	8	1	61	21.1
South America										6	8			14	20.6
NE Atlantic										2	2	8		12	22.2
Mediterranean-Black Sea											5	21	4	30	22.0
(Demir 1964, Turkey)							(1	1	2	38	351	558	49)	(1,000)	(21.6)
Gulf of Guinea-S. Africa											6	22		28	21.8
Total										14	67	59	5	145	21.4
Gymnosarda unicolor:															
Indian Ocean			4	3	2									9	13.8
W Pacific			2	16	3									21	14.1
Total			6	19	5									30	13.9
Allothunnus fallai					1	4	1	1						7	16.3

TABLE 11.—Number of second dorsal rays, dorsal finlets, and total second dorsal rays in species of Sardini.

Species	Second dorsal rays										Dorsal finlets							Total second dorsal rays										
	12	13	14	15	16	17	18	19	*N*	$\bar{x}$	6	7	8	9	10	*N*	$\bar{x}$	19	20	21	22	23	24	25	26	27	*N*	$\bar{x}$
Cybiosarda elegans						11	8	3	22	17.6			4	17	1	22	8.9							1	9	12	22	26.5
Orcynopsis unicolor:																												
E Mediterranean	1	6	16	7					30	14.0		3	22	11		36	8.2		1	4	16	7	1				29	22.1
Cent. Mediterranean		1	5	2					8	14.1			6	2		8	8.3			1	4	2	1				8	22.4
(Postel 1956a, Tunisia)												(7	140	42)		(189)	(8.2)											
Atlantic			3	2					5	14.4			6			6	8.0				3	2					5	22.4
Total	1	7	24	11					43	14.0		3	34	13		50	8.2		1	5	23	11	2				42	22.2
Sarda australis				5	11	3			19	15.9		15	4			19	7.2				4	9	6				19	23.1
Sarda chiliensis:																												
NE Pacific		4	10	15	6				35	14.7		5	28	2		35	7.9			5	10	14	6				35	22.6
(Kuo 1970)		(1	42	260	195	12)			(510)	(15.3)		(73	411	28)		(512)	(7.9)											
SE Pacific		3	18	9					30	14.2		12	18	1		31	7.6		1	8	14	7					30	21.9
(Kuo 1970)			(29	53	10)				(92)	(14.8)		(22	65	1)		(88)	(7.8)											
Total		7	28	24	6				65	14.4		17	46	3		66	7.8		1	13	24	21	6				65	22.3
Sarda orientalis:																												
Indian Ocean			1	5	4				10	15.3			9	1		10	8.1				1	4	5				10	23.4
NW Pacific			2	6	6	1			15	15.4		1	14			15	7.9				2	7	5	1			15	23.3
Cent. Pacific				2	2				4	15.5			3	1		4	8.3				1	2	—	1			4	23.3
E Pacific			1	7	8				16	15.4		1	12	3		16	8.1				2	3	11				16	23.6
Total			4	20	20	1			45	15.4		2	38	5		45	8.1				6	16	21	2			45	23.4
Sarda sarda:																												
North America		1	1	17	33	3	1		56	15.7		4	34	19		57	8.3				3	14	26	11	2		56	23.9
South America			1	3	8	2			14	15.8		1	9	4		14	8.2				1	2	7	4			14	24.0
NE Atlantic				1	7	2			10	16.1		1	6	4		11	8.3					1	5	3	1		10	24.4
Mediterranean-Black Sea				2	4	10	2		18	16.7		2	10	6		18	8.2					1	5	8	3	1	18	24.9
(Demir 1964, Turkey)		(2	4	17	87	114	25	1)	(250)	(16.5)	(1	15	530	439	15)	(1,000)	(8.5)											
Gulf of Guinea-S. Africa				2	7	13	5		27	16.8		7	18	2		27	7.8					3	7	15	2		27	24.6
Total		1	2	25	59	30	8		125	16.1		15	77	35		127	8.2				4	21	50	41	8	1	125	24.3
Gymnosarda unicolor:																												
Indian Ocean	1	7	1						9	13.0	1	8				9	6.9	2	6	1							9	19.9
W Pacific		13	9						22	13.4	2	20				22	7.0		15	7							22	20.3
Total	1	20	10						31	13.3	3	28				31	6.9	2	21	8							31	20.2
Allothunnus fallai	3	4							7	12.6	1	5	1			7	7.0	3	4								7	19.6

Cybiosarda has, modally, nine dorsal finlets; *Gymnosarda*, *Allothunnus*, and *S. australis* have seven; and the other four species have eight. Thus, in total number of second dorsal elements, *Cybiosarda* is high (25-27), *Gymnosarda* and *Allothunnus* are low (19-21), and the other species are intermediate.

Anal rays (Table 12) follow a similar trend to that of dorsal rays. *Cybiosarda* has many anal rays (15-17) and total anal elements (21-24). *Gymnosarda* has few anal rays (12-13) and total anal elements (18-19). Modally, *Cybiosarda*, *Orcynopsis*, *Allothunnus*, *Sarda chiliensis*, and *S. sarda* have seven anal finlets; *Gymnosarda*, *Sarda australis*, and *S. orientalis* have six finlets.

PECTORAL GIRDLE

The pectoral girdle consists of the girdle itself (cleithrum, scapula, and coracoid), the radials to which the pectoral fin rays attach and a chain of bones that connect the girdle onto the rear of the skull (posttemporal, supratemporal, supracleithrum, and two postcleithra).

Posttemporal

The posttemporal bones of the bonitos are generally similar with two anterior processes and a flat posterior body (Figure 58). The median process is thin and flat and articulates with the epiotic. The lateral process is rounded and rodlike and articulates with the intercalar anteroventrally. *Cybiosarda*, *Orcynopsis*, *Sarda*, and *Allothunnus* each have a well-developed shelf connecting the median and lateral processes while *Gymnosarda* (Figure 58e) has the shelf greatly reduced. The shelf extends posteriorly and forms a posteriorly directed spine beneath the body in all bonitos. *Cybiosarda*, *Orcynopsis*, and *Gymnosarda* have a shorter body than do *Sarda* and *Allothunnus*. There is a notch at the middle of the posterior edge of the body of the bone. The dorsal profile of the posttemporal is more or less flat in all the bonitos except in *Gymnosarda*, which has the margin convex posteriorly.

Supratemporal

The supratemporal bones of the bonitos are thin with two anterior processes and an elongated posterior body (Figure 59). The dorsal process lies free beneath the skin and the ventral process is firmly attached with connective tissue. The posterior body of the supratemporal overlaps externally the lateral process and part of the posterior body of the posttemporal. Lateral line canals are present on the internal surfaces of the

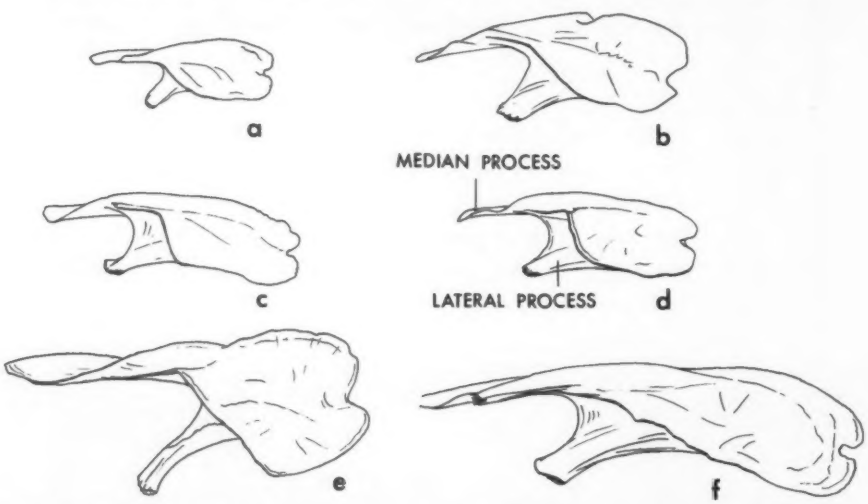


FIGURE 58.–External view of left posttemporals of six species of Sardini. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda sarda*, Tunisia, 504 mm FL. d. *Sarda australis*, New South Wales, 363 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 784 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

TABLE 12.—Number of anal rays, anal finlets, and total anal rays in species of Sardini.

Species	Anal rays										Anal finlets							Total anal rays								
	11	12	13	14	15	16	17	18	*N*	$\bar{x}$	5	6	7	8	9	*N*	$\bar{x}$	18	19	20	21	22	23	24	*N*	$\bar{x}$
Cybiosarda elegans					1	8	12		21	16.5		5	16			21	6.8				1	2	7	11	21	23.3
Orcynopsis unicolor:																										
E Mediterranean				1	17	9			27	15.3		9	23	2		34	6.8				1	25	1		27	22.0
Cent. Mediterranean				1	4	3			8	15.3		1	5	1		7	7.0					5	2		7	22.3
(Postel 1956a, Tunisia)												(16	150	23)		(189)	(7.0)									
Atlantic				1	3	1			5	15.0			5			5	7.0				1	3	1		5	22.0
Total				3	24	13			40	15.3		10	33	3		46	6.9				2	33	4		39	22.1
Sarda australis				1	14	4			19	15.2	1	17	1			19	6.0		1	—	13	5			19	21.2
Sarda chiliensis:																										
NE Pacific		2	11	17	5				35	13.7		10	23	2		35	6.8		3	16	12	4			35	20.5
(Kuo 1970)	(3	100	269	124	13)				(509)	(13.1)		(51	427	34)		(512)	(7.0)									
SE Pacific		2	10	17	2				31	13.6		18	12	1		31	6.4	1	5	14	10				30	20.1
(Kuo 1970)	(2	40	42	8)					(92)	(12.6)		(27	65)			(92)	(6.7)									
Total		4	21	34	7				66	13.7		28	35	3		66	6.6	1	8	30	22	4			65	20.3
Sarda orientalis:																										
Indian Ocean				3	7				10	14.7		8	2			10	6.2			1	9				10	20.9
NW Pacific				7	9				16	14.6		15	1			16	6.1			6	10				16	20.6
Cent. Pacific				2	2				4	14.5		4				4	6.0			2	2				4	20.5
E Pacific				4	10	2			16	14.9		12	4			16	6.3			1	12	3			16	21.1
Total				16	28	2			46	14.7		39	7			46	6.2			10	33	3			46	20.8
Sarda sarda:																										
North America				18	37	7			62	14.8		14	42	5		61	6.9			1	22	35	3		61	21.7
South America				2	10	2			14	15.0		3	11			14	6.8			1	2	10	1		14	21.8
NE Atlantic				1	9				10	14.9		2	7	1		10	6.9				3	6	1		10	21.8
Mediterranean-Black Sea				1	10	7			18	15.3		4	11	3		18	6.9				3	10	5		18	22.1
(Demir 1964, Turkey)			(2	8	66	88	24	5)	(193)	(15.7)	(2	98	730	164	6)	(1,000)	(7.1)									
Gulf of Guinea-S. Africa				2	9	14	2		27	15.6		8	19			27	6.7				5	9	13		27	22.3
Total				24	75	30	2		131	15.1		31	90	9		130	6.8			2	35	70	23		130	21.9
Gymnosarda unicolor:																										
Indian Ocean		6	3						9	12.4		9				9	6.0	6	3						9	18.4
W Pacific		4	17						21	12.8		21				21	6.0	4	17						21	18.8
Total		10	20						30	12.7		30				30	6.0	10	20						30	18.7
Allothunus fallai			3	4					7	13.6		2	5			7	6.7		1	3	3				7	20.3

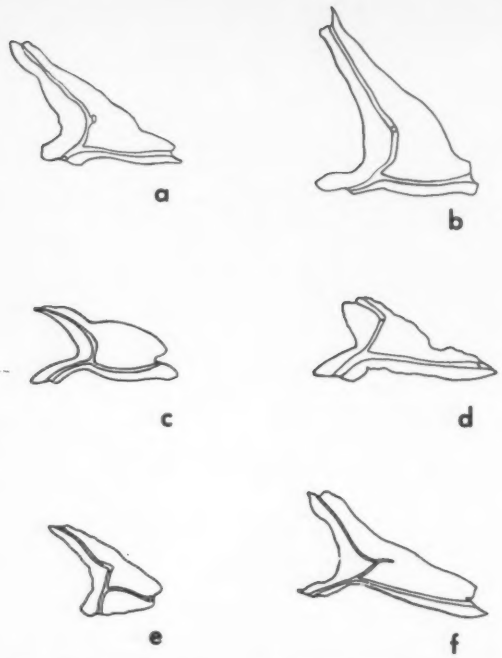


FIGURE 59.—Left supratemporals of six species of Sardini, external lateral view. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Tunisia, 503 mm FL. c. *Sarda sarda*, New Jersey, 375 mm FL. d. *Sarda chiliensis*, Peru, 473 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 607 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL.

supratemporal bones in all bonitos. *Orcynopsis*, *Cybiosarda*, and *Gymnosarda* have a shorter posterior body than do *Sarda* and *Allothunnus*. The thin edges of the supratemporal vary slightly among species of *Sarda* (Figure 59) and within each species of bonito. *Allothunnus* has the most elongate posterior body.

Supracleithrum

The supracleithrum lies in between the posttemporal and the cleithrum. *Cybiosarda*, *Orcynopsis*, and *Sarda* have relatively narrow and elongate supracleithra compared to *Gymnosarda* and *Allothunnus*. A dorsally projecting process is set off from the main body of the supracleithrum by a notch or angle on the anterodorsal part of the outer surface of the bone. *Sarda australis* and *Allothunnus* have the notch almost right-angled (Figure 60f, h). The other species of *Sarda* have a more poorly developed notch with a wider angle.

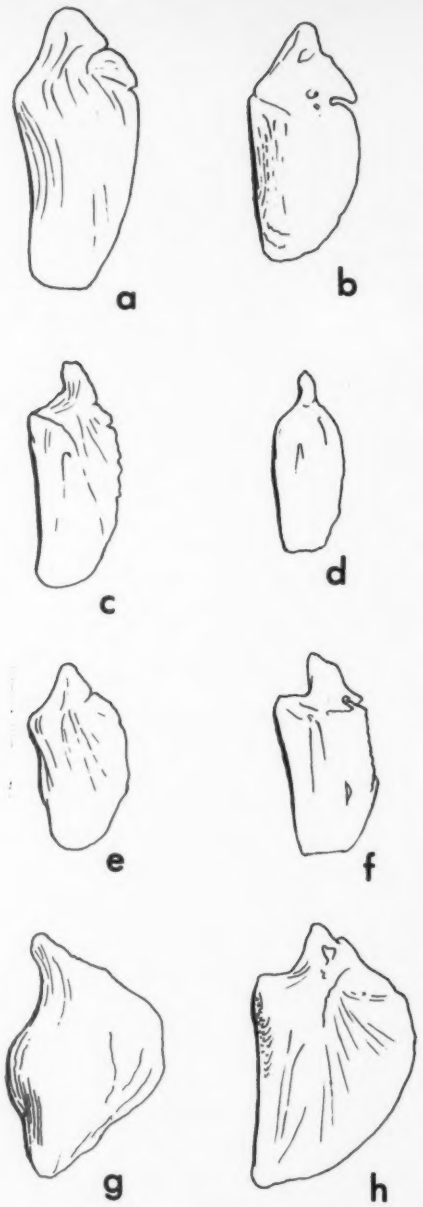


FIGURE 60.—Left supracleithra of eight species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda chiliensis*, Callao, Peru, 549 mm FL. d. *Sarda orientalis*, Panama, 415 mm FL. e. *Sarda sarda*, Tunisia, 504 mm FL. f. *Sarda australis*, New South Wales, 495 mm FL. g. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. h. *Allothunnus fallai*, California, 680 mm FL. a drawn twice as large as other figures.

Gymnosarda has a comparatively deep notch but the dorsally projecting process points more anteriorly than in any other bonito (Figure 60g). There is only a slight notch in *Cybiosarda* and no indentation at all on the anterodorsal edge of the bone in *Orcynopsis*. A ridge extends along the length of the inner surface of the supracleithrum. The ridge gradually merges into the main body of the bone dorsally. It stops abruptly about two-thirds of the way toward the dorsally projecting tip and is almost absent anteriorly in *Allothunnus*, as in *Thunnus*.

Cleithrum

The main body of the cleithrum in bonitos is crescent-shaped with an anterodorsal spine and a posteriorly projecting plate at the upper end, as in other scombrids (Figures 61, 62). The angle between the spine and the dorsal margin of the plate is smallest in *Gymnosarda* and widest, almost a right angle, in the species of *Sarda*. The angle is intermediate in *Cybiosarda*, *Orcynopsis*, and *Allothunnus*, similar to the condition in *Thunnus*. Godsil (1954) stated that the posteriorly projecting plate in *S. velox* (= *S. orientalis*) has a bluntly rounded distal end compared to *S. chiliensis*, which has the plate tapered distally. We found that this character is not consistent in *S. orientalis*, but *S. chiliensis* does have a more tapered distal portion than do the other species of *Sarda*. The main body of the cleithrum consists of an inner and an outer shelf, which join at the main axis, and a ridge at the anterior margin of the main axis on its inner surface. *Cybiosarda*, *Orcynopsis*, and *Sarda* have a poorly developed ridge along the anterior margin of the outer shelf (Figure 61a-d) as does *Thunnus* (de Sylva 1955, fig. 34). It is present only along the posterior edge of the upper two-thirds of the inner shelf of *Gymnosarda*. In *Allothunnus* (Figure 64f), the ridge becomes a broad well-developed inner shelf which extends internally from the outer shelf and at right angles to the inner shelf along the upper two-thirds of the main body. *Orcynopsis* has an expanded lower portion of the inner shelf; in

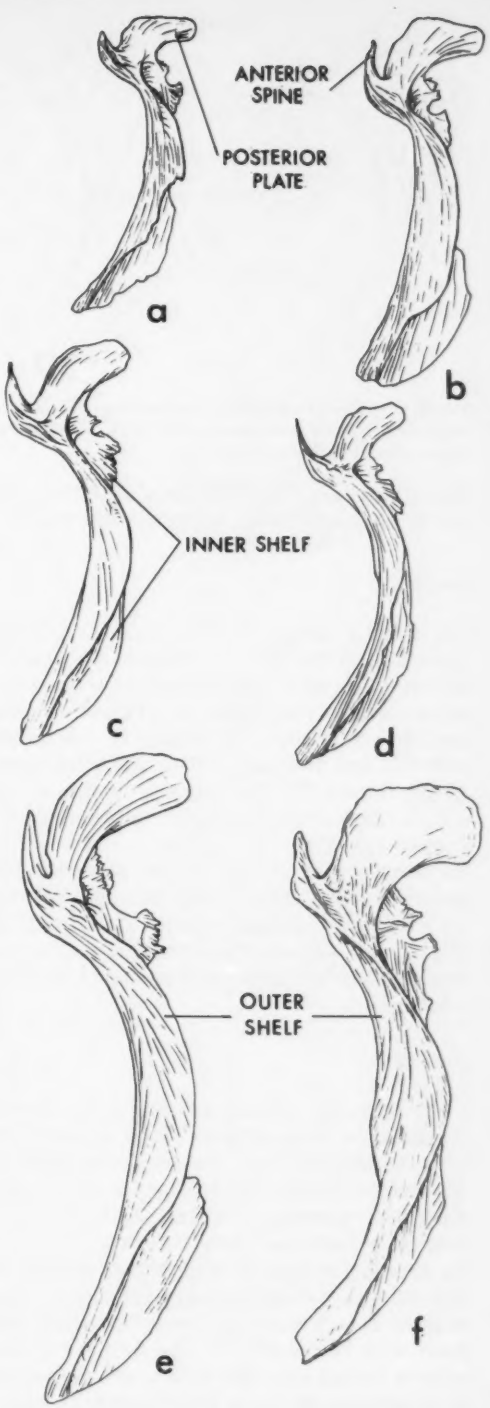


FIGURE 61.—Left cleithra of six species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 495 mm FL. c. *Sarda australis*, New South Wales, 495 mm FL. d. *Sarda chiliensis*, La Jolla, Calif., 453 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, Tasmania, 680 mm FL.

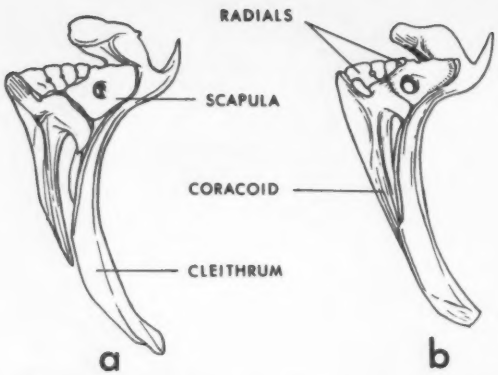


FIGURE 62.—Left pectoral girdles of two species of Sardini, internal view. a. *Sarda sarda*, Azores, 418 mm FL. b. *Cybiosarda elegans*, New South Wales, 360 mm FL.

Gymnosarda the inner shelf stops abruptly at the middle portion where the marginal ridge begins.

Scapula

The anterior margin of the scapula fits into the inner shelf of the cleithrum (Figure 62). This attachment extends to the posterior projecting plate anterodorsally. The scapula is attached with the coracoid posteriorly and dorsally it is attached with the first two and part of the third upper radials (Figure 63). The posterior margin of the scapula is drawn out into a facet which accepts the anterior ray of the pectoral fin. A suture bisects the scapula through the scapular fenestra. The general features of the scapula are similar among the bonitos. The scapular fenestra of *Gymnosarda* (Figure 63e) is relatively larger, and that of the species of *Sarda* (Figure 63c, d) is smaller, than the other bonitos.

Coracoid

The coracoid is elongated and more or less triangular in shape (Figure 63). It is connected with the scapula along its flat dorsal edge in *Allothunnus* (Figure 63f). In all other bonitos, this margin is interrupted ventral to the scapular fenestra and extends dorsally as an interdigitating suture. The ventral wing of the coracoid is xiphoid with a V-shaped depression along the midline. The coracoid has two points of attachment with the cleithrum, the first along the anterior margin near the scapula, and the second at the anterior end of the ventral wing. The margin of the coracoid, between its articulations with the cleithrum, is curved inward. This curvature is more pronounced in *Gymnosarda* (Figure 63e) than in the other bonitos, which resemble *Thunnus*.

Radials

The four radials differ in size and shape and are attached directly to the thickened posterior edges of the scapula and coracoid (Figures 62, 63). The size of the radials increases ventrally. Two small foramina are located between the second and third, and the third and fourth radials, counting downward. The first two radials and the upper half of the third radial attach to the coracoid; the ventral half of the third plus the fourth radial attach to the scapula. A fenestra is present between the dorsoposterior end of the coracoid and the largest radial, which has a prominent posteroventral process in all bonitos except *Sarda* and *Allothunnus*. In both characters, the fenestra and the last radial process, *Sarda* and *Allothunnus* resemble *Thunnus*; the other bonitos resemble *Acanthocybium*.

Pectoral Fin Rays

The first (and largest) pectoral ray articulates directly with a posterior process of the scapula. The other rays attach to the radials. Within the Scombridae, the number of pectoral fin rays increases from the more primitive members of the family to the more advanced: Scombrini 18-21, Scomberomorini 20-25, Sardini 21-28, Thunnini (except for *Thunnus*) 22-29, *Thunnus* 30-36. Within the Sardini (Table 13), *Orcynopsis* and *Cybiosarda* have the fewest pectoral fin rays (modes of 22 and 23, respectively). *Gymnosarda* has the most (25-28), followed by one species of *Sarda* (*S. australis*, 25-27), and *Allothunnus* (24-26). The other three species of *Sarda* are intermediate with species modes of 24 or 25.

Postcleithrum 1 and 2

The posterior projecting plate of the cleithrum has its posterior end attached to the curved first postcleithrum, which connects to another bone, the second postcleithrum. Both postcleithra are thin and bent. Postcleithrum 1 (the upper one) has a narrow anterodorsal end and a broad posteroventral body (Figure 64). *Gymnosarda* has a pointed

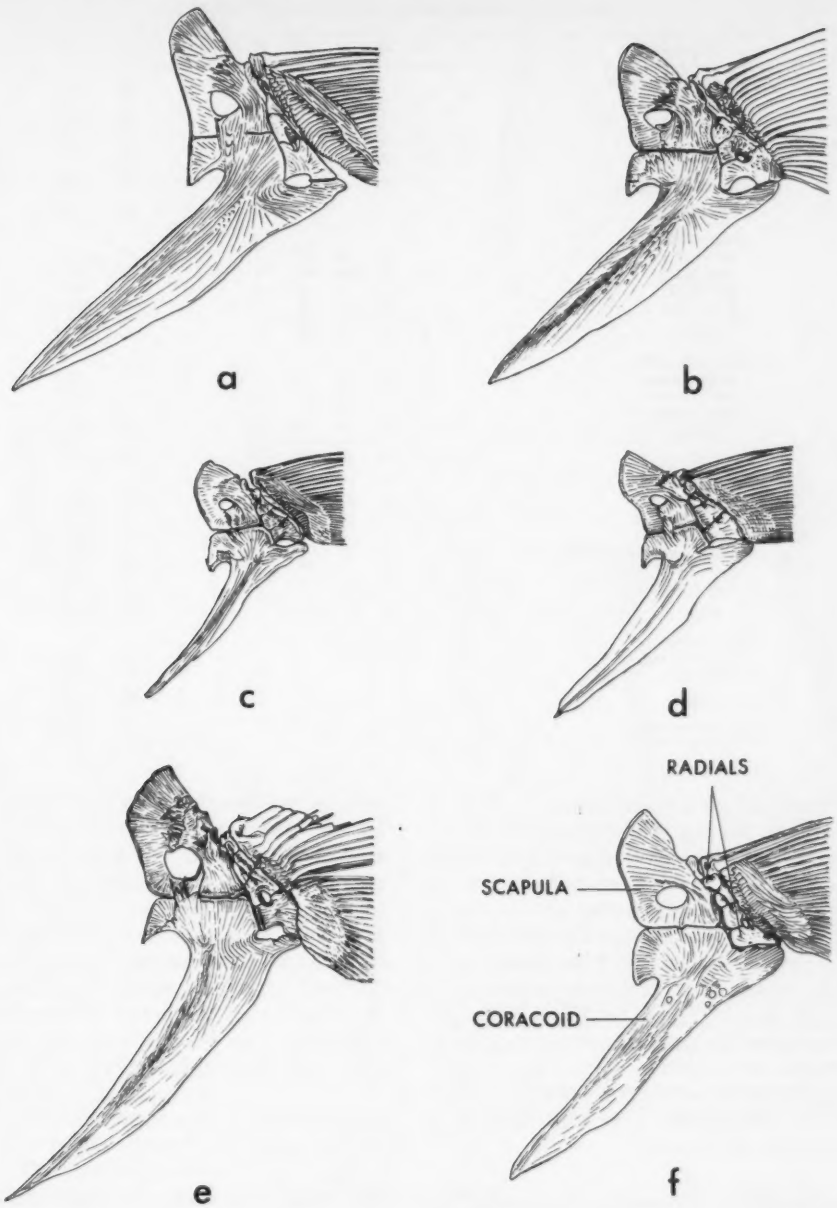


FIGURE 63.—Left pectoral girdles (minus cleithra) of six species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda chiliensis*, California, 472 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, California, 680 mm FL. a drawn twice as large as b-f.

TABLE 13.—Number of pectoral rays in species of Sardini.

Species	21	22	23	24	25	26	27	28	N	$\bar{x}$
Orcynopsis unicolor:										
E Mediterranean	6	17	7						30	22.0
Cent. Mediterranean		5	3						8	22.4
Atlantic		3	5						8	22.6
Total	6	25	15						46	22.2
Cybiosarda elegans		1	15	5					21	23.2
Sarda australis					6	9	4		19	25.9
Sarda chiliensis:										
NE Pacific		1	6	9	12	3			31	24.3
(Kuo 1970)		(1	28	226	229	25	1)		(510)	(24.5)
SE Pacific		2	4	13	10	3			32	24.2
(Kuo 1970)			(6	41	44	1)			(92)	(24.4)
Total		3	10	22	22	6			63	24.3
Sarda orientalis:										
Indian Ocean			2	4	2	1			9	24.2
NW Pacific			2	10	3				15	24.1
Cent. Pacific				2	2				4	24.5
E Pacific			2	6	6				14	24.3
Total			6	22	13	1			42	24.2
Sarda sarda:										
North America			9	27	21	4			61	24.3
South America			1	3	3	1			8	24.5
NE Atlantic				4	5	2			11	24.8
Mediterranean-Black Sea			2	11	5				18	24.2
(Demir 1964, Turkey)		(1	12	51	34	7)			(105)	(24.3)
Gulf of Guinea-S. Africa			6	13	7				26	24.0
Total			18	58	41	7			124	24.3
Gymnosarda unicolor:										
Indian Ocean					3	5	—	1	9	25.9
W Pacific					3	8	9	1	21	26.4
Total					6	13	9	2	30	26.2
Allothunnus fallai				2	1	3			6	25.2

anterodorsal end on postcleithrum 1, which is unique among bonitos. Postcleithrum 1 in *Orcynopsis* and *Cybiosarda* is elongate and broad at the upper end. The general features of postcleithrum 1 of *Sarda* species are similar to those of *Thunnus*. *Allothunnus* has the broadest postcleithrum 1. Postcleithrum 2 (the lower one) is a spinelike structure with both ends pointed and a broad upper process (Figure 65). These bones are similar in all bonitos except for minor variations. Postcleithrum 2 of *Gymnosarda* has an elongate upper end and a curved lower portion. The broad process of postcleithrum 2 is much enlarged in *Allothunnus* as in *Thunnus*.

PELVIC GIRDLE

The pelvic fin rays (I, 5) attach directly to the paired basipterygia which make up the pelvic girdle. The bones are fused together along the midline and are imbedded in the ventral abdominal wall free from connections with any other bones. Each basipterygium is composed of three main parts (Figure 66): a wide anterodorsal plate and two processes: an anterior process (anterior xiphoid process of de Sylva 1955) and a shorter, stronger, posteriorly directed styliform process (posterior xiphoid process of de Sylva 1955). There are three wings to the anterodorsal plate (Kishinouye 1923): external, internal, and vertical (ventral). Anteriorly, the external wing turns into the same vertical plane and merges into the vertical wing. The internal wing and the external wing meet in one plane posteriorly along a ridge. A "valleylike" depression is present in the posterior half of the anterodorsal plate in all the bonitos except *Allothunnus* (Figure 66f). The internal wing of *Allothunnus* attaches to the vertical wing horizontally at a right angle which is completely separate from the external wing, as in *Thunnus* (de Sylva 1955, figs. 50-52). The vertical wing is the largest and most variable character of the bonito basipterygium. The vertical wings of *Orcynopsis*, *Cybiosarda*, and *Sarda* are elongate and have pointed anterior ends. *Gymnosarda* and *Allothunnus* have vertical wings that are shorter

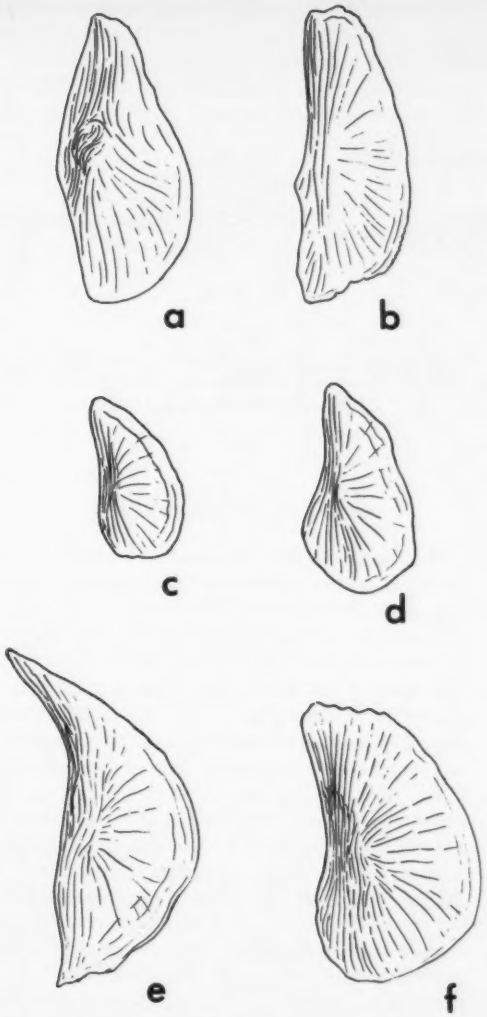


FIGURE 64.–Left first postcleithra of six species of Sardini. a. *Cybiosarda elegans*, New South Wales, 360 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 774 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

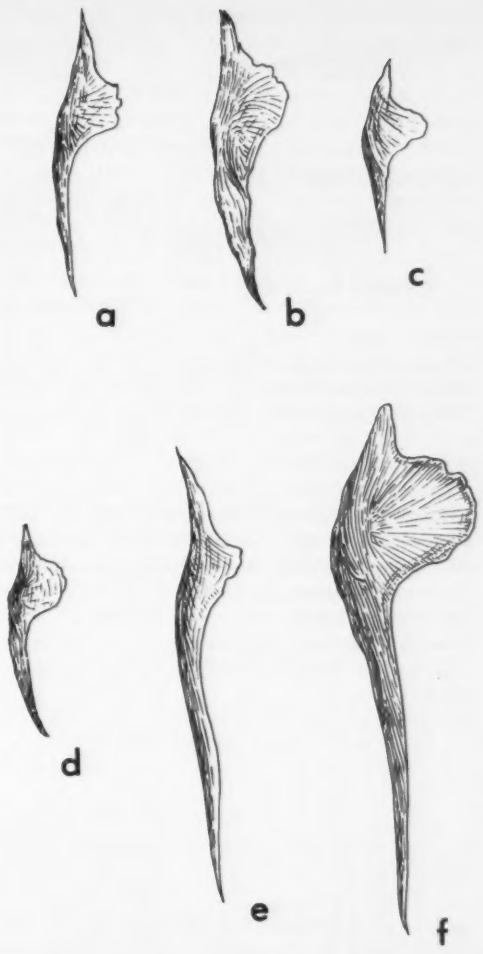


FIGURE 65.–Left second postcleithra of six species of Sardini, external lateral view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 545 mm FL. c. *Sarda sarda*, New Jersey, 375 mm FL. d. *Sarda orientalis*, Jalisco, Mexico, 434 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 607 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

and broader in the midanterior portion. The portion above the internal wing is even better developed in *Allothunnus* than in *Thunnus* (de Sylva 1955, fig. 51). The internal and external wings of *Allothunnus* are less prominent than in the other bonitos. Among the species of *Sarda*, *S. orientalis* has a narrower and longer vertical wing.

The anterior process of the basipterygium extends anteriorly to about the middle of the anterodorsal plate. The posterior styliform process is shorter and stronger than the anterior process in the bonitos. Except for *Gymnosarda*, no differences were found among the bonitos in the fleshy bifid interpelvic process that is supported by the paired posterior styliform process of the basipterygia

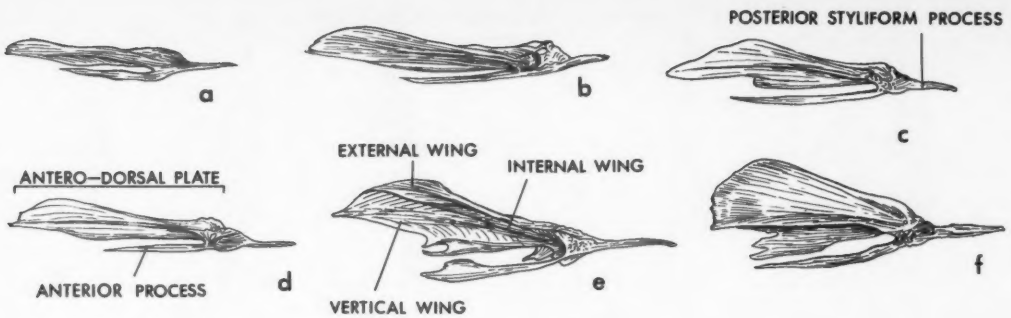


FIGURE 66.–Lateral view of inner surface of right basipterygium of pelvic girdles of six species of Sardini. a. *Cybiosarda elegans*, Western Australia, 442 mm FL. b. *Orcynopsis unicolor*, Tunisia, 620 mm FL. c. *Sarda chiliensis*, Callao, Peru, 437 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL.

(Figure 67). *Gymnosarda* differs from the other bonitos in having a single interpelvic process. *Auxis* and *Grammatorcynus* also have a single interpelvic process, the former very large, the latter small. However, there is a posterior styliform process from each basipterygium regardless of whether the fleshy interpelvic process is single or bifid.

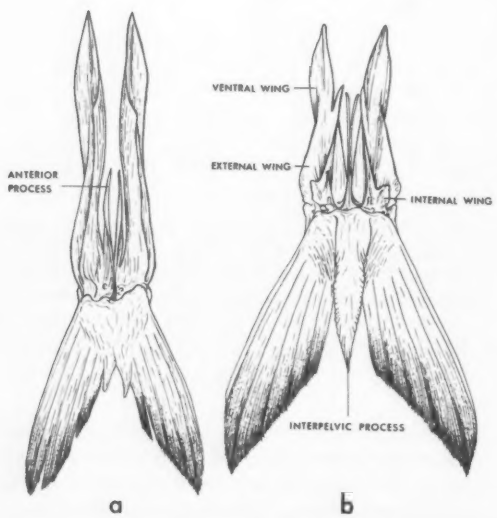


FIGURE 67.–Ventral view of pelvic girdles and fins of two species of Sardini. a. *Orcynopsis unicolor*, Tunisia, 495 mm FL. b. *Gymnosarda unicolor*, Truk Islands, 787 mm FL. a drawn twice as large as b.

PART 2. SYSTEMATICS

The family Scombridae can be divided into two subfamilies: the Gasterochismatinae, which contains only the aberrant *Gasterochisma melampus* Richardson, and the Scombrinae. The Scombrinae is composed of two groups of tribes (Figure 68). The more primitive mackerels (Scombrini – *Scomber* and *Rastrelliger*) and Spanish mackerels (Scomberomorini–*Grammatorcynus*, *Scomberomorus*, and *Acanthocybium*) have a distinct notch in the hypural plate, lack any bony support for the fleshy caudal peduncle keels (Figure 56), and do not have preural centra two and three greatly shortened. The bonitos comprise a tribe (Sardini, Starks 1910) of five genera and eight species. The bonitos differ from the higher tunas (Thunnini–*Auxis*, *Euthynnus*, *Katsuwonus*, and *Thunnus*) in lacking any trace of a specialized subcutaneous vascular system, in lacking dorsally projecting lateral cartilaginous ridges on the tongue, and in having the bony caudal keel only partially developed instead of complete. The Sardini lack the prominent paired frontoparietal foramina characteristic of the Thunnini (except *Auxis*). Except for *Allothunnus*, the Sardini also differ from the Thunnini in lacking prominent prootic pits. In this character, and in its tiny conical teeth, *Allothunnus* is similar to the Thunnini. The Sardini agree with *Thunnus* and with the Scombrini and Scomberomorini in lacking the bony shelf that divides the neural canal of the anterior six vertebrae into dorsal and ventral portions. This bony division is characteristic of the

other three genera of Thunnini–*Katsuwonus*, *Euthynnus*, and *Auxis*.

Five genera, four of them monotypic, are recognized as a result of analyzing the morphology described in the first part of this paper. A sample of some of the more important characters is summarized in Table 14. *Orcynopsis* and *Cybiosarda* form a pair of related genera in characters such as the poor development of the bony caudal keels, location of the spleen, presence of a pair of tooth patches fused to the glossohyal bone, and length of the liver lobes. They differ sharply in vertebral number; *Orcynopsis* usually has 18 precaudal plus 20 caudal vertebrae compared to (22-23) + (24-25)=47 in *Cybiosarda*. In some respects, *Sarda* and *Gymnosarda* also form a pair of related genera. However, characters of *Gymnosarda* such as the well-developed swim bladder, curved sagitta, large number of olfactory laminae, paired glossohyal tooth plates, location of the spleen, lack of cephalic intermuscular bones, and parhypural fused to the hypural plate demonstrate that *Gymnosarda* is very different from the other genera of Sardini. *Allothunnus* differs strongly from the other bonitos in liver shape, presence of prootic wings, and shape of pineal foramen, but shares more characters in common with the Sardini than with the Thunnini as previously noted.

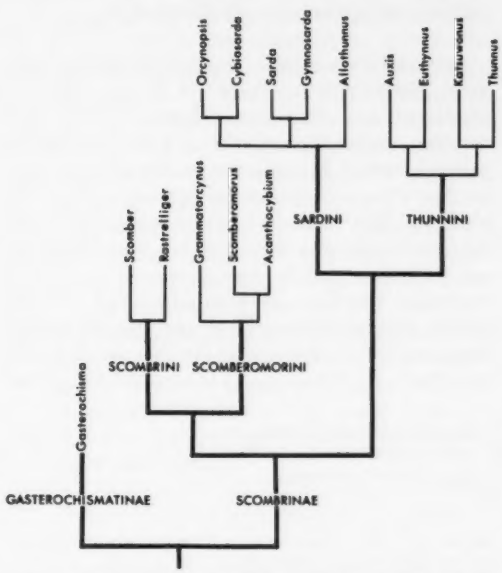


FIGURE 68.–The subfamilies, tribes, and genera of the Scombridae.

Orcynopsis Gill

Orcynopsis Gill 1862:125 (type-species *Scomber unicolor* Geoffroy St. Hilaire; misspelled *Orycnopsis*).

TABLE 14.–Summary of characters distinguishing the five genera of Sardini.

Character (reference)	*Orcynopsis*	*Cybiosarda*	*Sarda*	*Gymnosarda*	*Allothunnus*
Intestine (Fig. 5)	folded	folded	straight	folded	straight
Tongue teeth (Fig. 43)	2 patches fused to glossohyal	2 patches fused to glossohyal	none	2 patches free from glossohyal	none
Prootic pit	absent	absent	absent	absent	present
Prootic wings	absent	absent	absent	absent	present
Bony caudal keels (Fig. 55)	low and poorly developed	low and poorly developed	well-developed and divided into 2 parts	well-developed and divided into 2 parts	low and poorly developed
Length of liver lobes (Fig. 4)	right lobe longest	right lobe longest	right and left lobes equally long	right and left lobes equally long	3 subequal lobes
Spleen (in ventral view) (Fig. 3)	small and concealed under liver	small and concealed under liver	large and prominent posteriorly	present on right side anteriorly	not visible
Cephalic intermuscular bones	1 on each side of skull	1 on each side of skull	2	none	1
Pineal foramen (Fig. 10-14)	elongate and slit-shaped	elongate and slit-shaped	elongate and slit-shaped	elongate and slit-shaped	large and oval
Swim bladder	absent	absent	absent	well-developed	absent
Sagitta	flat	flat	flat	curved	flat
Opercular bones (Fig. 45-47)	not elongate	not elongate	not elongate	elongate	not elongate
Olfactory laminae (Table 3)	25-28	28-33	21-39	48-56	28-30
Vertebrae (Table 9)	18+20=38	(22-23)+(24-25)=47	43-46; 50-55	19+19=38	20+19=39
Pectoral rays (Table 13)	22-23	23-24	23-26	25-27	24-26
Dorsal spines (Table 10)	12-14	16-17	17-23	13-15	15-18
Parhypural (Fig. 56)	free from hypural plate	free from hypural plate	free from hypural plate	fused to hypural plate	free
Interpelvic process (Fig. 67)	small paired processes	small paired processes	small paired processes	single large process	small and paired
Total first arch gill rakers (Table 7)	12-17	12-15	8-27	11-14	72-80

Pelamichthys Giglioli 1880:25 (type-species *Scomber unicolor* Geoffroy St. Hilaire by original designation).

Comparative Diagnosis.–The monotypic genera *Orcynopsis* and *Cybiosarda* share several important characters that distinguish them from *Sarda* and *Gymnosarda*: low and poorly developed bony caudal keels versus well-developed caudal keels divided into anterior and posterior sections; right lobe of liver longest versus right and left lobes much longer than the middle lobe; spleen small and not visible in ventral view versus large and prominent in ventral view. Both genera have high first dorsal fins (Figure 1a, b) and are relatively more compressed (almost like *Scomberomorus*) than fusiform. *Orcynopsis*, *Cybiosarda*, and *Gymnosarda* have two patches of tongue teeth, but the patches are attached to the glossohyal bone in *Orcynopsis* and *Cybiosarda* and are on separate plates that fit over the glossohyal in *Gymnosarda*.

Orcynopsis differs from *Cybiosarda* most obviously in lacking the bold pattern of stripes and blotches on the body of the latter. *Orcynopsis* has lower counts than does *Cybiosarda*: vertebrae 37-39 vs. 47-48; dorsal spines 12-14 vs. 16-18; second dorsal rays 12-15 vs. 17-19; pleural ribs 16 vs. 20; and intermuscular bones 19-20 vs. 24-25.

Orcynopsis unicolor is a short-bodied and short-headed species (Table 15). It has a shorter snout-anal and snout-second dorsal distance than do other bonitos. The snout-first dorsal and snout-pelvic fin origin distances are shorter than in other bonitos except *Gymnosarda unicolor* and *Sarda australis*. The snout-pectoral fin origin, pelvic fin insertion-vent, and pelvic fin tip-vent distances are all shorter than in other bonitos except *Gymnosarda*. The fins are high compared to fork length, the second dorsal and anal fins are higher than in other bonitos except for the second dorsal in *Cybiosarda*. The bases of the second dorsal and

TABLE 15.–Comparison of morphometric characters of three populations of *Orcynopsis unicolor*. First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

	Israel			Lebanon			Tunisia		
Character	Range	$\bar{x}$	N	Range	$\bar{x}$	N	Range	$\bar{x}$	N
Fork length (mm)	285-735	404	12	242-325	287	11	312-645	539	7
Fork length									
Snout — A	555-597	577	12	573-598	587	11	556-597	578	7
Snout — 2D	481-522	499	12	496-530	511	11	400-503	481	7
Snout — 1D	239-253	247	12	248-262	253	11	229-257	246	7
Snout — P_2	265-282	273	12	276-293	284	11	263-285	270	7
Snout — P_1	231-243	238	12	240-257	247	11	219-239	229	7
P_1 — P_2	109-116	113	7	118-129	122	11			
Head length	226-246	235	12	239-251	243	11	224-241	231	7
Max. body depth	221-268	246	11	240-272	255	11	226-248	240	7
Max. body width	106-140	124	9	113-135	123	11	116-139	130	7
P_1 length	125-153	138	12	131-140	135	11	135-148	142	7
P_2 length	57- 68	63	12	55- 64	61	11	62- 66	64	6
P_2 insertion - vent	278-307	294	12	266-296	288	11	280-315	300	7
P_2 tip - vent	218-241	230	12	209-242	228	11	216-241	233	7
Base 1D	235-255	246	10	241-259	248	11	230-255	241	7
Height 2D	109-148	128	10	108-124	117	10	116-150	126	7
Base 2D	107-126	117	12	107-140	133	11	108-149	120	7
Height anal	111-148	126	10	107-126	118	11	119-131	125	7
Base anal	94-128	114	11	98-131	111	10	95-120	106	7
Caudal spread	236-275	261	6	249-297	270	10	239-259	244	5
Snout (fleshy)	76- 95	89	11	92- 98	94	11	90- 94	91	6
Snout (bony)	65- 80	76	11	77- 83	80	11	76-111	83	7
Maxilla length	101-118	113	11	116-129	123	11	104-119	112	6
Post orbital	109-115	112	7	113-122	117	11			
Orbit (fleshy)	24- 32	28	11	29- 34	31	11	23- 66	31	7
Orbit (bony)	46- 58	51	11	53- 61	57	11	44- 69	52	7
Interorbital width	65- 74	68	11	59- 70	66	11	67- 83	72	6
Head length									
Snout (fleshy)	327-405	381	11	376-392	387	11	385-406	396	6
Snout (bony)	280-353	326	11	316-335	328	11	329-480	358	7
Maxilla length	431-508	483	11	485-517	505	11	456-495	483	6
Post orbital	453-490	478	7	462-515	484	11			
Orbit (fleshy)	107-133	121	11	120-137	129	11	98-121	107	7
Orbit (bony)	204-249	218	11	221-254	236	11	192-222	211	6
Interorbital width	256-308	289	11	239-288	272	11	262-310	297	6

anal fins are longer than in any bonitos except *Cybiosarda*.

Orcynopsis unicolor Geoffroy St. Hilaire

Scomber unicolor E. Geoffroy St. Hilaire 1817: pl. 24, fig. 6 (original description). I. Geoffroy St. Hilaire 1827:331-332 (description; Alexandria, Egypt). Guichenot 1850:58-59 (description; Algeria).

Cybium commersoni (not of Lacépède, 1800). Bonaparte 1845:74 (listed after Verany; Italy).

Cybium Bonapartii Verany 1847:493 (original description; Genoa, Italy).

Pelamys Bonaparte. Filippi and Verany 1859:194 (description, comparison with *S. sarda*), fig. 4. Moreau 1881:434-436 (synonymy, description; very rare, Nice). Liebman 1934:325 (Israel).

Pelamys unicolor. Günther 1860:368 (synonymy, description). Canestrini 1870:103 (description, rare in Italian waters). Rochebrune 1882:95-96 (Senegal). Stassano 1890:32-33 (Spanish Sahara). Griffini 1903:398-399 (synonymy; description; Italy).

Cybium altipinne Guichenot in Duméril 1858:262 (nomen nudum, listed; Senegal).

Orycnopsis unicolor. Gill 1862:126 (original description of *Orcynopsis*, misspelled *Orycnopsis*).

Thynnus peregrinus Collett 1879a:20-30 (original description; Christiania (now Oslo) Norway), pl. 1.

Orcynopsis unicolor. Collett 1879b:1-3 (*Thynnus peregrinus* Collett a synonym of *O. unicolor*). Ninni 1882:264 (Adriatic). Dresslar and Fesler 1889:434-435 (description; synonymy). Vinciguerra 1890:98-100 (synonymy; Cabo Blanco, Spanish West Africa). Carus 1893:659-660 (synonymy; description). Gruvel and Bouyat 1906:150 (Cabo Yubi to Cabo Blanco, Spanish West Africa). Lozano 1916:298-302 (description; Melilla, Spanish Morocco). Parona 1919:91-95 (synonymy, description; Italy), pl. 10-11. Ehrenbaum 1924:12 (Alexandria). Chabanaud 1925:197-200 (comparison with *Sarda* and *Gymnosarda*), fig. 1 (lingual and pharyngeal teeth), 2 (vomerine teeth). Chabanaud and Monod 1927:278-279 (common; Port Étienne, Mauritania), fig. 30B. Buen 1930a:46-47 (description, synonymy), pl. 2, fig. 5. Dieuzeide 1930:141-144 (synonymy, description, Algeria). Buen and Frade 1932:72 (in key), fig. 5. Frade and Buen 1932:70 (in key). Le Gall 1934a:288 (description), fig. (after Smitt). Jensen 1937:11-12 (Collett's 1879 records from the Skagerak). Fraser-Brunner 1950:148-149 (description), fig. 14. Postel 1950:63-66 (description; reproduction; food; length-weight; Cape Verde), 64 (fig. of viscera). Lozano y Rey 1952:527-531 (description), pl. 40, fig. 1, col. pl. 41, figs. 2 and 3. Morice 1953a:37 (dentition; gill rakers), 41 (generic key). Postel 1954:357-358 (stomach contents), 359 (parasites), 361 (gonosomatic index). Dieuzeide et al. 1955:145-146 (description, fig.; Algeria). Dollfus 1955:55 (listed), 141 (references to occurrence in Atlantic Morocco; Rabat market). Frade and Postel 1955:35 (gonads; spawning season; Cape Verde), fig. 6 (ovary). A. Postel 1955:59-60, 65, table 2, fig. 2 (number of teeth on upper and lower jaws, 100 Tunisian specimens). Postel 1955b:31-32 (sex ratio by months, maximum size by sexes, number of eggs). Postel 1956a:1220-1248 (synonymy, relationships, distribution, morphometry, meristics, anatomy, reproduction, food, parasites), fig. 3 (distribution map), fig. 4 (drawing), figs. 9, 10 (viscera). Postel 1956b:52 (common names). Postel 1956c:67-68 (abundant in Gulf of Gabes, Tunisia). Tortonese 1956:7 (Mediterranean). Postel 1960:257 (distribution). Collette and Gibbs 1963a:26 (relationships). Šoljan 1963:147-148 (description; figs.; Adriatic Sea). George et al. 1964:21 (rare, Lebanon). Postel 1964:220 (listed, North Africa). Collette 1966:370 (*Cybium altipinne* a synonym of *O. unicolor*). Zharov 1967:220 (relationships of scombroids). Bini 1968:39-40 (synonymy; description), color plate. Williams 1968:436 (Ghana). Blache et al. 1970:375 (in key; fig. 961, not fig. 960 which is *Scomberomorus tritor*). Collette 1970:4 (Israel). Ben-Tuvia 1971:20 (Israel). De Groot and Nijssen 1971:8 (Arguin Bank, Mauritania). Lozano Cabo 1970:158 (North Africa). Economidis 1972:526 (Greece). Magnuson 1973:350 (maximum size, no swim bladder, short pectoral fin). Postel 1973:474-475 (range, synonymy).

Pelamichthys unicolor. Giglioli 1880:25 (original description of *Pelamichthys*, Italy).

Cybium Veranyi. Giglioli 1880:25 (description, Italy).

Sarda unicolor. Smitt 1892:102-104 (synonymy; description; rare in Scandinavia), fig. 29. Fowler 1936:625-626 (synonymy; description;

compiled), fig. 283 (after Smitt). Cadenat 1937:482 (Sénégal). Navarro 1943:131 (Arguin Bank, Mauritania), pl. 19, fig. B (photograph). Tortonese 1949:65 (permanent resident, Mediterranean Sea). Tortonese and Trotti 1949:87 (Ligurian Sea).

Types of Nominal Species.–*Scomber unicolor* E. Geoffroy St. Hilaire 1817: pl. 24, fig. 6. No type-specimens, text published by Isidore Geoffroy St. Hilaire in 1827 ". . . sont extraits des notes prises en Egypte par mon pére. Je n'ai pu me procurer ni cette especé, ni celle qui est figurée dans l'Atlas sous le nom de *Maquereau unicolore*; . . . trouvee dans le Méditerranée."

Cybium Bonapartii Verany 1847:493. The type was examined in the Museo della R. Universita di Genova by Collett (1879b) and the name placed in the synonymy of *O. unicolor* (along with *Thynnus peregrinus* Collett). The present whereabouts of the type, if extant, are unknown. It is not listed in the type catalog of the Museo Civico di Storia Naturale di Genova (Tortonese 1963) which absorbed the University collections. The original description was based on a specimen from the Genoa market taken on 31 May 1847. It had eight dorsal finlets, seven anal finlets, conical teeth, and lacked spots on the body.

Cybium altipinne Guichenot in Duméril 1858. Apparently a nomen nudum as there is no description and we cannot find a description by either Guichenot or Duméril elsewhere. Also considered a nomen nudum by Postel (1973). Previous authors (Fraser-Brunner 1950; Bauchot and Blanc 1961) have considered *C. altipinne* to be a synonym of *Scomberomorus tritor* (Cuvier) but the specimen labelled as type is clearly *O. unicolor* as Collette (1966) has shown.

Thynnus peregrinus Collett 1879a:20-30, pl. 1. Placed in the synonymy of *Orcynopsis unicolor* later in the same year (Collett 1879b). Lectotype (herein selected): ZMO J4632; 565 mm FL; Norway, Christianiafjord (Oslo), Naesøen; 26 Aug. 1876. Prof. Esmark. Paralectotype: ZMO J4631; 570 mm; same data as lectotype. The smaller syntype is selected as lectotype because the dorsal spine count of 13 matches the original description and because the two patches of teeth on the tongue are the usual size for *O. unicolor*. The paralectotype has two very small patches of tongue teeth. Counts for the lectotype (paralectotype in parentheses): dorsal fin rays XIII + 14 + VIII (XIV + 14 + VIII); anal fin rays 15 + VII (15 + VII); pectoral fin rays (left-right) 23-21 (23-22); gill rakers 3 + 1 + 11 = 15 in both; upper jaw teeth (left-right) 23-25 (20-22); lower jaw teeth 20-20 (16-17).

Distribution.–*Orcynopsis unicolor* is an eastern Atlantic endemic whose range is centered in the Mediterranean Sea but extends south to Dakar, Sénégal and north to Oslo, Norway (Figure 69). It was first described from Egypt by Geoffroy St. Hilaire (1817) and most subsequent records have come from the southern Mediterranean: Lebanon (George et al. 1964; 12 USNM specimens), Israel (Liebman 1934; Collette 1970; Ben-Tuvia 1971; 5 USNM specimens; SFRS 1686, 2009, BT-1767, BT-1582, BT-1986), Egypt (Ehrenbaum 1924; 10 NHMV specimens), Tunisia (Postel 1956c; 7 USNM specimens), Algeria (Guichenot 1850; Dieuzeide 1930; Dieuzeide et al. 1955), and Morocco (Lozano 1916). Records from the northern Mediterranean are scarcer: Genoa, Italy (Verany 1847; MSNG 1987); Ligurian Sea (Tortonese and Trotti 1949); Adriatic Sea (Ninni 1882; Šoljan 1963; MSUF 495D); Elba (MSUF coll. 1172); Nice, France (Moreau 1881; NHMV 1884.I.204). The Norwegian record is based on the two types of *Thynnus peregrinus* Collett, taken at Naesøen, Christianiafjord (= Oslofjord) in August 1876. There are several records for the Atlantic coast of North Africa south to Dakar, Sénégal: Rabat, Morocco (Dollfus 1955); Spanish West Africa (Stassano 1890; Vinciguerra 1890; Gruval and Bouyat 1906); Mauritania (Chabanaud and Monod 1927; Navarro 1943; de Groot and Nijssen 1971; USNM uncat.); and Cape Verde and Dakar, Sénégal (Duméril 1858; Rochebrune 1882; Postel 1950; Frade and Postel 1955; MNHN A.5797). There is one record from further south, in the Gulf of Guinea. Williams (1968:436) reported that a specimen was taken off Ghana during the Guinean Trawling Survey. The specimen was apparently not saved, the identification was probably based on the first draft of the illustrated key by Blache et al. (1970) which has the figures of *Scomberomorus tritor* and *Orcynopsis unicolor* transposed, and the record is well out of the normal range of the species. Therefore, the record must be considered highly questionable unless confirmed by additional specimens.

Cybiosarda Whitley

Scomberomorus (*Cybiosarda*) Whitley 1935:236 (type-species *S.* (*C.*) *elegans* Whitley by monotypy).

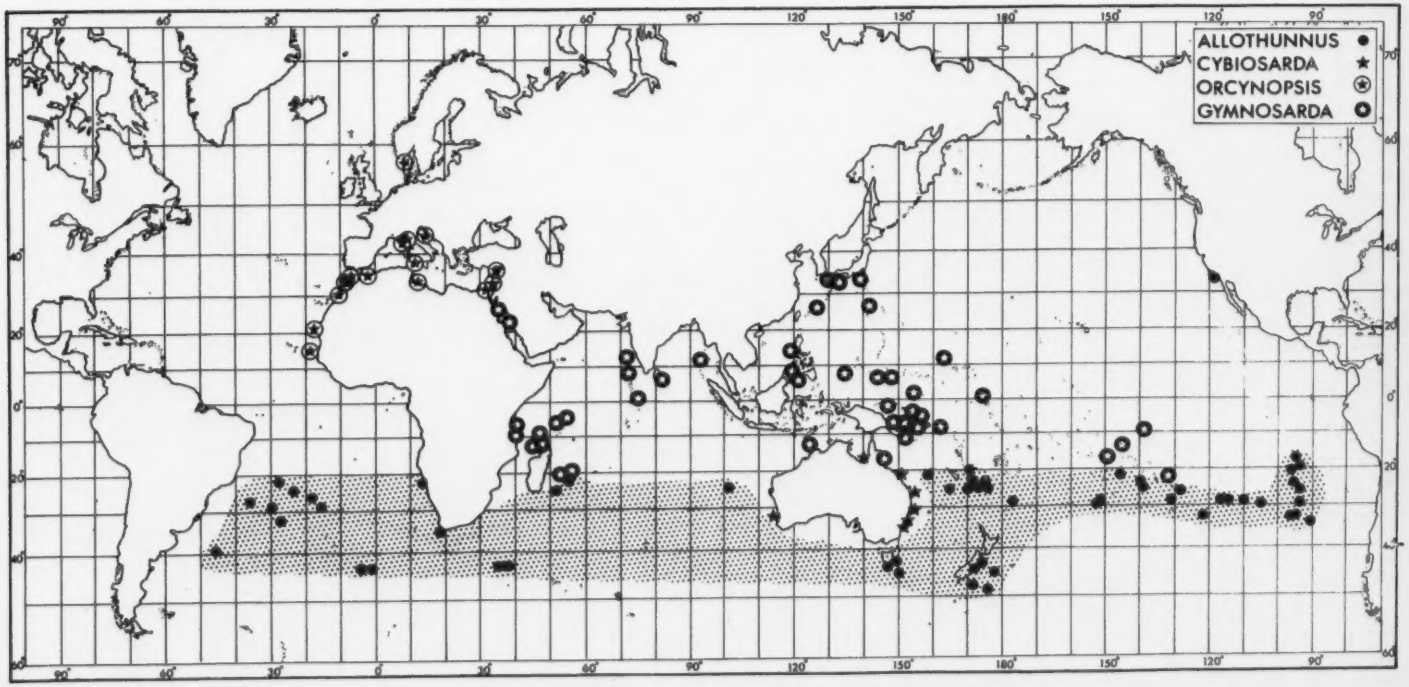


FIGURE 69.—Distribution of *Orcynopsis unicolor*, *Gymnosarda unicolor*, *Cybiosarda elegans*, and *Allothunnus fallai* based on specimens personally examined and literature records.

Comparative Diagnosis.–The monotypic genera *Cybiosarda* and *Orcynopsis* share several characters that distinguish them from *Sarda* and *Gymnosarda*: low and poorly developed bony caudal keels instead of well developed, but divided into anterior and posterior parts; right lobe of liver much longer than middle and left lobes instead of both right and left lobes elongate; spleen small and not visible in ventral view versus spleen large and prominent in ventral view. Both have one intermuscular bone on the back of the skull compared to none in *Gymnosarda* and two in *Sarda*. Both genera have high first dorsal fins and are relatively more compressed (almost like *Scomberomorus*) than fusiform. *Orcynopsis*, *Cybiosarda*, and *Gymnosarda* have a pair of tooth patches on the tongue, but these are attached to the glossohyal bone in the first two genera and are on separate plates that fit over the glossohyal in *Gymnosarda*. Osteologically, the two genera also show many similarities.

Cybiosarda differs from *Orcynopsis* most obviously in its prominent pattern of blotches above the lateral line and stripes below it (Figure 1a). *Cybiosarda* has higher counts than does *Orcynopsis*: vertebrae 47-48 vs. 37-39; dorsal spines 16-18 vs. 12-14; second dorsal rays 17-19 vs. 12-15; pleural ribs 19 vs. 16; and intermuscular bones 23-24 vs. 19-20. *Cybiosarda* has a smaller sagitta with a longer and thinner rostrum than does *Orcynopsis*.

Cybiosarda is a relatively short-bodied bonito (Table 16). The snout-second dorsal distance is shorter than in other bonitos except *Orcynopsis* and *Sarda chiliensis*, the first dorsal fin base is shorter than in the others except *Orcynopsis* and *Gymnosarda*. The second dorsal and anal fins are higher than in *Sarda* and *Allothunnus* and the second dorsal fin is also higher than in *Gymnosarda*.

TABLE 16.–Morphometric characters of *Cybiosarda elegans*. First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

Character	Range	$\bar{x}$	N
Fork length (mm)	250-422	347	19
Fork length			
Snout — A	638-678	652	19
Snout — 2D	509-547	531	18
Snout — 1D	260-284	273	19
Snout — P_2	289-317	299	18
Snout — P_1	258-291	267	18
P_1 — P_2	113-136	125	18
Head length	259-280	266	19
Max. body depth	199-252	227	16
Max. body width	105-168	133	17
P_1 length	128-148	138	19
P_2 length	76- 88	82	19
P_2 insertion - vent	344-363	327	17
P_2 tip - vent	240-282	262	17
Base 1D	229-270	254	19
Height 2D	101-118	108	19
Base 2D	112-133	121	18
Height anal	97-118	107	18
Base anal	82-100	91	19
Caudal spread	219-275	251	16
Snout (fleshy)	94-104	98	19
Snout (bony)	79- 87	82	19
Maxilla length	125-140	130	19
Post orbital	128-146	136	19
Orbit (fleshy)	26- 34	29	19
Orbit (bony)	54- 61	58	9
Interorbital width	65- 78	73	19
Head length			
Snout (fleshy)	352-383	367	19
Snout (bony)	299-323	308	19
Maxilla length	475-501	489	19
Post orbital	489-551	511	19
Orbit (fleshy)	98-125	109	19
Orbit (bony)	204-232	218	9
Interorbital width	244-292	273	19

Cybiosarda elegans (Whitley)

Scomberomorus (*Cybiosarda*) *elegans* Whitley 1935:236-237 (original description; Moreton Bay, Queensland, Australia).

Cybiosarda elegans. Whitley 1936:42-45 (redescription of type; anatomy; pl. 4, fig. 1; text fig. 5; Queensland). Whitley 1939:274 (New South Wales). Serventy 1941a:43 (description, New South Wales and Western Australia), pl. 4, bottom fig. Whitley 1948:24 (listed; Western Australia). La Monte 1952:48, 50 (description). Munro 1958a:113-114 (description; Queensland, New South Wales, Western Australia), fig. 756 (after Serventy). Jones and Silas 1961:379 (compiled), fig. 5 (after Fraser-Brunner). Collette and Gibbs 1963b:28 (description), pl. 7 (after Fraser-Brunner). Jones and Silas 1963:1786-1787 (compiled). Jones and Silas 1964:24-25 (description). Marshall 1964:357-358 (summary), col. pl. 52, fig. 345. Whitley 1964a:228-229 (summary), pl. 2, fig. b (Western Australia specimen), text fig. 4c (distribution). Whitley 1964b:48 (listed). Marshall 1966:204, col. pl. 52. Grant 1972:113 (description; Queensland), fig. (after Serventy).

Gymnosarda elegans. Fraser-Brunner 1950:149 (description), fig. 15.

Types.–*Scomberomorus* (*Cybiosarda*) *elegans* Whitley 1935:236-237. Original description repeated with additional locality data and the QM catalog number for the type plus more information on the species by Whitley (1936). Holotype: QM

I.5413; 356 mm FL; Queensland, Moreton Bay, Goat Island; G. W. Watson. A second specimen (QM I.5142) is labelled as a paratype and is mentioned as having been collected with the first specimen by Whitley (1936:42). However, it is not mentioned in the original description where the statement is made "Described from a specimen in the Queensland Museum from Moreton Bay, Queensland"; therefore, it should not be considered as a paratype. Counts for the holotype: dorsal fin rays XVI+17+IX; anal fin rays 17+VII; pectoral fin rays (left-right) 24-24; gill rakers 4+10=14; upper jaw teeth (left-right) 17-20; lower jaw teeth 12-12.

Distribution.–*Cybiosarda elegans* is restricted to the northern three quarters of Australia (Figure 69). It was first described by Whitley (1935) from Moreton Bay, Queensland, and then reported from New South Wales by Whitley (1939) and from Western Australia by Serventy (1941a). We have examined specimens from near Perth, Western Australia, and several localities along the east coast (Shellharbour and Maclean, New South Wales, and Moreton Bay and Lindeman Island, Queensland). In addition, we have examined a 250-mm specimen (AMS I.15557-095) taken by the CSIRO shrimp survey in the Gulf of Carpentaria at lat. 16°40'S, long. 139°50'E.

Sarda Cuvier

Sarda Cuvier 1829:199 (type-species *Scomber sarda* Bloch 1793 by monotypy).

Pelamys Cuvier in Cuvier and Valenciennes 1831:149 (type-species *Scomber sarda* Bloch 1793 by original designation).

Palamita Bonaparte 1831:173 (substitute name for *Pelamys* Cuvier 1831 preoccupied by *Pelamys* Oken 1816 in Reptilia, Hydrophiidae; therefore, takes the same type-species *Scomber sarda* Bloch 1793).

Creotroctes Gistel 1848:p. x (type-species *Scomber sarda* Bloch 1793; substitute name for *Sarda* Cuvier 1829).

Comparative Diagnosis.–The species of *Sarda* all have several stripes dorsally, ranging from horizontal to oblique in orientation. *Sarda* (and *Allothunnus*) differ from the other genera of bonitos in having the intestine run straight from the stomach to the anus (versus having two additional loops, Figure 5) and two intermuscular bones on each side of the back of the skull (*Gymnosarda* has none, the other three genera have one on each side).

Sarda and *Gymnosarda* share a number of characters that distinguish them from *Orcynopsis* and *Cybiosarda*: the bony caudal peduncle keels are well developed as in higher tunas, but are divided into anterior and posterior sections on each vertebra; the spleen is large and prominent in ventral view versus small and not visible in ventral view; the right and left lobes of the liver are both much longer than the middle lobe versus only the right lobe elongate. Both *Sarda* and *Gymnosarda* are fusiform in body shape instead of being more laterally compressed.

Sarda (Figure 1c) differs from *Gymnosarda* (Figure 2a) in being completely covered with fine scales posterior to the corselet (instead of being naked posteriorly); in lacking a swim bladder; in having the spleen centrally located in the posterior half of the body cavity in ventral view (instead of on the right side of the anterior half); in having fewer lamellae in the olfactory rosettes (21-39 vs. 48-56); more vertebrae (42-55 vs. 38); and in lacking a pair of tooth patches on the glossohyal bone.

Species of *Sarda*.–Four allopatric species of *Sarda* are recognized based on the morphological characters described in the first part of this paper (a summary of 26 of these characters is presented in Table 17). *Sarda australis* is similar to the other three species in the genus in 11-15 characters. *Sarda chiliensis* and *S. orientalis* resemble each other in 12 characters. *Sarda sarda* stands out as being very different from *S. chiliensis* and *S. orientalis*, sharing only eight or nine characters with each. Many of the meristic differences between *S. sarda* and the other species of *Sarda* are correlated with its greater number of body segments as reflected by having 50-55 vertebrae (compared to 43-46). Thus, *S. sarda* also has more dorsal spines, pleural ribs, intermuscular bones, vertebral keels, and the first closed haemal arch is further posterior. *Sarda sarda* is most similar to *S. australis* in numbers of anal rays, gill rakers, upper and lower jaw teeth, occasional presence of vomerine teeth, angle of the hyomandibular spine and the condyle, width of the supramaxilla, and relative length of the haemal pre- and post-zygapophyses on the first caudal vertebra. If the several differences between *S. australis* and *S. sarda* that are correlated with the higher number of body segments are considered as one character, the two species would appear even more similar.

TABLE 17.–Summary of characters distinguishing the four species of *Sarda*.

Character (reference)	*S. sarda*	*S. australis*	*S. chiliensis*	*S. orientalis*
Lamellae in nasal rosettes (Table 3)	22-33 ($\bar{x}$ 26.5)	34-39 ($\bar{x}$ 37.2)	21-30 ($\bar{x}$ 25.4)	25-36 ($\bar{x}$ 31.9)
Vomerine teeth present	sometimes	sometimes	never	never
Upper jaw teeth (Table 5)	16-26	16-26	18-30 ($\bar{x}$ 23.5)	12-20 ($\bar{x}$ 15.5)
Lower jaw teeth (Table 6)	12-24 ($\bar{x}$ 16.0)	11-20 ($\bar{x}$ 14.5)	14-25 ($\bar{x}$ 19.2)	10-17 ($\bar{x}$ 13.0)
Palatine teeth	8-21 ($\bar{x}$ 12.3)	7-14 ($\bar{x}$ 10.7)	9-22 ($\bar{x}$ 15.2)	8-19 ($\bar{x}$ 11.9)
Supramaxilla width (Fig. 32)	intermediate	intermediate	wide	narrow
Ectopterygoid-dorsal portion (Fig. 36)	pointed	pointed	pointed	slightly expanded
Hyomandibular spine-condyle (Fig. 39)	projects beyond condyle	short	short	projects beyond condyle
Angle of hyomandibular spine (Fig. 39)	about 90°	about 90°	greater than 90°	less than 90°
Elliptical ceratohyal window (Fig. 42)	present	present	present	only slight depression
Ventral surface of glossohyal (Fig. 43)	depression present	depression present	depression present	no depression
Gill rakers (Table 7)	16-23	19-21	23-27	8-13
Vertebrae (Table 9)	50-55	43-46	43-46	43-46
Pleural ribs	24	19-23	19-23	19-23
Intermuscular bones	31-45	32-36	32-36	32-36
Keels on vertebrae number	5-10	5-8	5-8	5-8
First closed haemal arch (Fig. 51)	13th-15th vertebra	13th-15th vertebra	12th-14th vertebra	12th-14th vertebra
Length of haemal prezygapophyses and postzygapophyses at precaudal-caudal junction (Fig. 52)	postzygapophyses longer than prezygapophyses	postzygapophyses longer than prezygapophyses	prezygapophyses longer than postzygapophyses	prezygapophyses longer than postzygapophyses
Dorsal spines (Table 10)	20-23	17-19	17-19	17-19
Dorsal finlets (Table 11)	modally 8	modally 7	modally 8	modally 8
Anal rays (Table 12)	14-17 (modally 15)	14-17 (modally 15)	12-15 (modally 14)	14-16 (modally 15)
Anal finlets (Table 12)	modally 7	modally 6	modally 7	modally 6
Total anal elements (Table 12)	19-23 (modally 21-22)	19-23 (modally 21-22)	18-22 (modally 20)	20-22 (modally 21)
Supracleithral notch (Fig. 60)	wide angle	almost 90°	wide angle	wide angle
Pectoral rays (Table 13)	23-26	25-27 (modally 26)	22-26 (modally 24-25)	22-26 (modally 24-25)
Vertical wing of pelvic girdle (Fig. 66)	shorter and wider	shorter and wider	narrower and longer	narrower and longer

Sarda australis (Macleay)

Pelamys australis Macleay 1880:557 (original description; Port Jackson, Sydney, Australia). Ogilby 1887:29 (listed, New South Wales; should be compared with *P. chilensis*). McCoy 1888:208 (compared with *P. schlegeli*). Stanbury 1969:206 (holotype in Macleay Museum, University of Sydney).

Pelamys schlegeli McCoy 1888:207-208 (original description from one specimen from Prince Phillip Bay, Victoria), col. pl. 155.

Pelamys chilensis (not of Cuvier, 1831). Ogilby 1893:97-98 (synonymy, description; New South Wales), pl. 26.

Sarda chilensis (not of Cuvier 1831). Waite 1904:42 (listed, New South Wales). Stead 1906:163-164 (New South Wales and Victoria), fig. 59. Stead 1908:94-95 (New South Wales), pl. 54.

Sarda chiliensis (not of Cuvier 1831). McCulloch 1922:105 (New South Wales), pl. 33, fig. 291a.

Sarda orientalis (not of Temminck and Schlegel 1844). Lord 1927:15 (listed, Tasmania).

Sarda australis. Walford 1936:9 (in key as valid species of *Sarda*). Serventy 1941a:42-43 (description; Eastern Australia), pl. 4, middle fig. Serventy 1941b:7 (summer visitor to Victoria). Laevastu and Rosa 1963:1844 (fig. 7, map of distribution and fishing areas, in part). Whitley 1964a:236 (common from the Capricorn Islands, Great Barrier Reef to Sydney), fig. 2 (distribution map). Whitley 1964b:48 (listed).

Sarda chiliensis australis. Roughley 1951:121-122 (description; Australia), plate 49b. Munro 1958a:113 (description; Queensland, New South Wales, and Victoria), fig. 754. Grant 1972:114 (description; Queensland), fig. (after McCoy).

Sarda chilensis australis. Silas 1964:296 (in key, map, *S. chilensis* divided into an eastern Pacific *S. c. chilensis* and an Australian *S. c. australis*).

Comparative Diagnosis.–*Sarda australis* shows 11-15 similarities each, among characters considered (Table 17), with *S. sarda*, *S. chiliensis*, and *S. orientalis*. It differs from all of them in having slightly fewer pectoral rays (25-27, modally 26 vs. 22-26, modally 24-25) and in having a 90° angle in

the supracleithral notch instead of a much wider angle. *Sarda australis* resembles *S. sarda* in characters such as the numbers of anal rays, gill rakers, and upper and lower jaw teeth, occasional presence of vomerine teeth (vs. never), having a 90° angle between the hyomandibular spine and condyle, having the haemal postzygapophyses longer than the prezygapophyses at the precaudal-caudal vertebral junction, and having a supramaxilla of intermediate width between the wide one in *S. chiliensis* and the narrow one in *S. orientalis*. *Sarda australis* resembles *S. chiliensis* in having a short hyomandibular spine that does not project beyond the condyle.

Morphometrically (Tables 1, 18), *Sarda australis* is very similar to the other species of *Sarda*. It has a longer first dorsal fin base (315-343 thousandths of FL) than either *S. chiliensis* (267-314) or eastern Pacific *S. orientalis* (282-302) but overlaps with Indo-West Pacific *S. orientalis* (285-327) and *S. sarda* (291-330). The maxilla is longer (503-539 thousandths of head length) than in *S. chiliensis* (460-503).

Types.–*Pelamys australis* Macleay 1880:557. Holotype: AMS Macleay Mus. F-333; 405 mm FL; Australia, New South Wales, Sydney, Port Jackson. Counts: dorsal fin rays XIX + 16 + VII; anal fin rays 15 + VI; pectoral fin rays 25-25; gill rakers 6 + 1 + 13 = 20; upper jaw teeth (left-right) 14-19; lower jaw teeth 13-10; palatine teeth about 10 in one long row; vertebrae 24 + 21 = 45; head length 82.9 mm, maxilla length 43.2 mm.

Distribution.–*Sarda australis* has the most restricted range of any species of bonito: the east coast of Australia plus Norfolk Island (Figure 70). Munro (1958a) gave the range as Queensland, New South Wales, and Victoria. Whitley (1964a) stated that *S. australis* ". . . is common at practically all times off eastern Australia from about the Capricorns [Queensland] to Sydney or even Gabo Island . . ." [just south of New South Wales–Victoria border]. There are specific literature reports from Victoria (McCoy 1888; Serventy 1941b) and Tasmania (Lord 1927), as well as from New South Wales. Except for one specimen from Norfolk Island (AMS I.10751), all the material we have examined has come from New South Wales (from north to south: Macleay River, Broughton Island off Port Stephens, Laurieton, New Castle, Sydney, Woolongong). Sherrin (1886) and others have reported *Sarda* from New Zealand, but it seems likely that these reports were based on misidentified specimens of *Allothunnus fallai* which was not described until 1948.

TABLE 18.–Morphometric characters of *Sarda australis*. First set of numbers are measurements expressed in thousandths of fork length, second set as thousandths of head length.

Character	Range	$\bar{x}$	N
Fork length (mm)	195-526	349	21
Fork length			
Snout — A	662-698	674	20
Snout — 2D	581-605	586	20
Snout — 1D	251-276	263	20
Snout — P_2	281-312	296	20
Snout — P_1	258-281	267	20
P_1 — P_2	104-125	116	19
Head length	259-279	267	20
Max. body depth	221-240	231	16
Max. body width	127-169	141	17
P_1 length	112-135	121	19
P_2 length	76-118	85	20
P_2 insertion - vent	340-393	374	18
P_2 tip - vent	260-311	290	18
Base 1D	315-343	326	20
Height 2D	77-95	86	19
Base 2D	88-118	103	20
Height anal	72- 92	81	20
Base anal	48- 88	78	20
Caudal spread	238-277	259	11
Snout (fleshy)	88-103	96	20
Snout (bony)	76- 88	81	20
Maxilla length	131-150	139	20
Post orbital	120-136	130	20
Orbit (fleshy)	32- 41	37	19
Orbit (bony)	56- 84	66	20
Interorbital width	58- 72	66	19
Head length			
Snout (fleshy)	342-381	361	20
Snout (bony)	291-324	305	20
Maxilla length	503-539	518	20
Post orbital	478-508	492	20
Orbit (fleshy)	134-148	137	19
Orbit (bony)	231-267	246	20
Interorbital width	226-266	249	19

Sarda chiliensis (Cuvier)

Two subspecies of *S. chiliensis* are recognized: *S. c. chiliensis* (Cuvier) for the southeastern Pacific population and *S. c. lineolata* (Girard) for the northeastern Pacific population.

Sarda chiliensis chiliensis (Cuvier)

Pelamys chiliensis Cuvier in Cuvier and Valenciennes 1831:163 (original description; Valparaiso, Chile).

Pelamys chilensis. Günther 1860:368 (in part; description).

Sarda chilensis. Starks 1906:784 (Callao, Peru). Meek and Hildebrand 1923:318-319 (in part; description; Peru). Hildebrand 1946:372-374 (description; 13 Peruvian

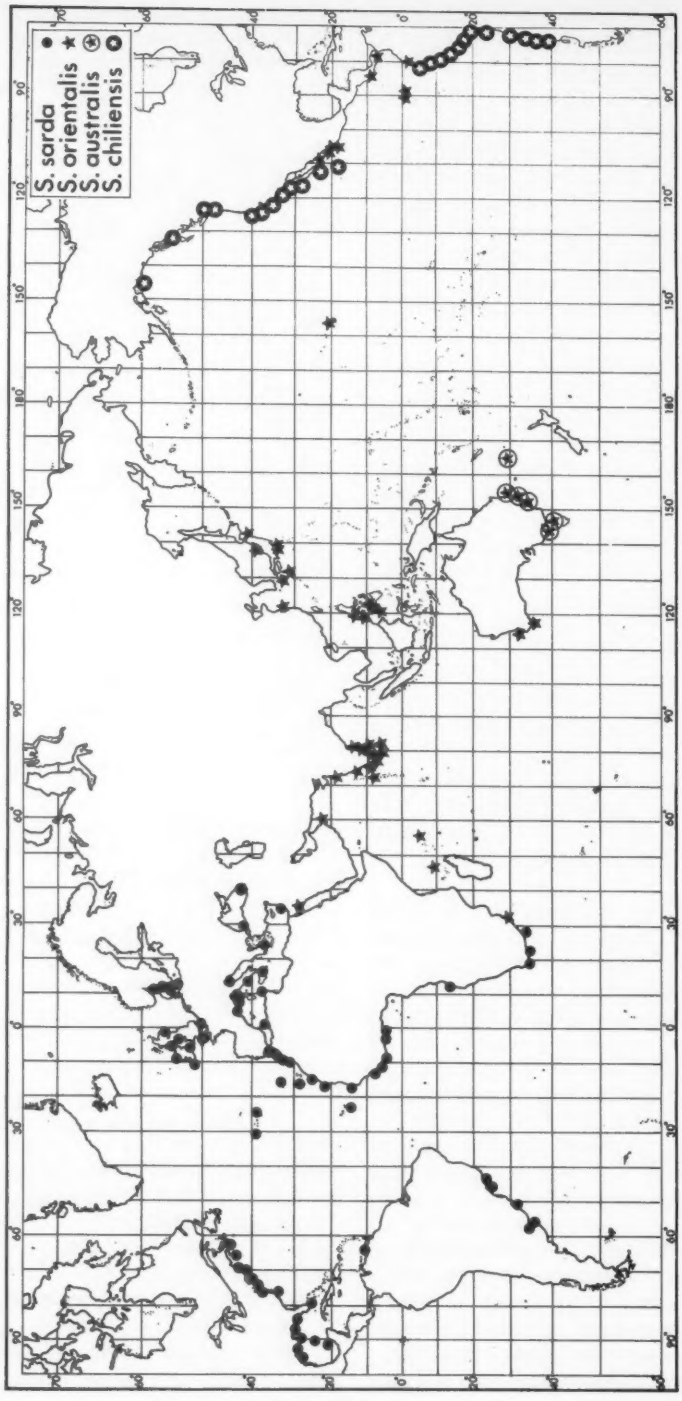


FIGURE 70.—Distribution of the four species of *Sarda* based on specimens personally examined and literature records.

specimens [USNM]). Fraser-Brunner 1950:146-147 (in part). La Monte 1952:44 (description), pl. 15. Mann 1954:298 (description, distribution; Chile). Vildoso 1960:1-75 (sexual maturity and reproduction; Peru). Bauchot and Blanc 1961:373 (type of *P. chiliensis*). Ancieta 1963:1607-1619 (fishery in Peru). Laevastu and Rosa 1963:1844, (fig. 7, in part; map of distribution and fishing areas). Vildoso 1963a:1143-1152 (reproduction; Peru). Blanc and Bauchot 1964:449, fig. 21 (type of *P. chiliensis*). Ancieta 1964:17-49 (species synopsis; Peru).

Sarda chiliensis. Walford 1936:8-10 (description; comparison with other species of *Sarda*). Chabanaud 1944:1-6 (in part; description; synonymy; all Indo-Pacific species considered synonyms of *S. chiliensis*). Godsil 1955:7-21, figs. 1-6, table 1-3 (description; anatomy; 5 Peruvian specimens). Pinkas 1961:175-188 (in part; 8 Peruvian juveniles, 38.0-201 mm). Klawe 1961b:487-493 (in part; juveniles from Peru and Chile), fig. 4 (160-mm Peruvian specimen).

Sarda sarda chiliensis. Buen 1958:12-17 (synonymy; description; fishery; range south to Talcahuano, Chile). Chirichigno 1969:75 (common name), 79 (fig. 147).

Sarda chilensis chilensis. Vildoso 1963b:1549-1556 (Peru; subspecifically distinct from *S. c. lineolata* based on vertebral number). Silas 1964:296-297 (in key, map, *S. chilensis* divided into an eastern Pacific *S. c. chilensis* and an Australian *S. c. australis*).

Sarda sarda chilensis. Sánchez and Lam 1970:42-43 (length-weight; weights of parts of body; fig. of vertebral column; photograph; Peru).

Sarda chiliensis chiliensis. Kuo 1970:2805-2806 (taxonomy, growth, maturation).

Sarda chiliensis lineolata (Girard)

Pelamys lineolata Girard 1859:106 (original description, San Diego, Calif.).

Pelamys chilensis. Günther 1860:368 (in part).

Sarda chilensis. Jordan and Gilbert 1882:428 (in part; description; synonymy). Jordan and Evermann 1896:872-873 (in part; description; synonymy). Starks 1910:91-93 (osteology; Puget Sound specimen). Meek and Hildebrand 1923:318-319 (in part; description; synonymy). Hildebrand 1946:374 (*S. lineolata* a synonym of *S. chilensis*). Fraser-Brunner 1950:146 (in part). Morice 1953a:37-39 (dentition; number of gill rakers and vertebrae). Ricker 1959b:6 (Revillagigedos Island, new record).

Sarda lineolata. Walford 1936:8-10 (key to species of *Sarda*; description). Walford 1937:22-23 (description). Clothier 1950:52-53 (vertebrae), pl. 10 (vertebral column). Godsil 1954:30-43, figs. 12-19, tables 4-5 (anatomy). Clemens and Wilby 1961:226-227 (description; north to northern end of Vancouver Island), fig. 131. Manzer 1965:853-855, fig. 1 (description; record from east coast of Vancouver Island).

Sarda stockii David 1943:31-33 (original description; Santa Monica Mountains, Calif.; Modelo formation, Upper Miocene), pl. 4 (holotype), 155 (additional specimen from Lompoc).

Sarda chiliensis. Chabanaud 1944:1-6 (description, in part; recognizes Atlantic *S. sarda* and Indo-Pacific *S. orientalis*). Fraser-Brunner 1950:146 (in part). Godsil 1955:38-42 (*S. lineolata* a synonym of *S. chiliensis*). Pinkas 1961:175-188 (in part; 27 juveniles 16.7-54.5 mm, from California and Baja California), fig. 4 (16.7-mm juvenile), fig. 5 (33.0-mm juvenile). Klawe 1961b:487-493 (in part; juveniles from California and Baja California), fig. 3 (42-mm juvenile). Radovich 1961:22, 31 (records north of Point Conception). Klawe 1962:180 (92-mm juvenile, Baja California). Laevastu and Rosa 1963:1844 (fig. 7, in part, map of distribution and fishing areas). Fitch and Craig 1964:201 (fig. 4, outline of sagitta), 202 (sagittae of three species of *Sarda* almost identical). Quast 1964:448 (11 specimens from coastal Alaska). Patten et al. 1965:298-299 (Puget Sound records). Magnuson and Prescott 1966:54-67 (courtship, locomotion, feeding). Fierstine and Walters 1968:1-31 (vertebral counts, myology, aspect ratio of caudal fin). Magnuson and Heitz 1971:363-365 (gill raker apparatus and filtering area). Pinkas et al. 1971:64-82 (food habits in southern California and Baja California). Hart 1973:373-374 (description, distribution, fig.).

Sarda chiliensis lineolata. Kuo 1970:2805-2806 (taxonomy, growth, maturation).

Comparative Diagnosis.—*Sarda chiliensis* is most similar to *S. orientalis* and *S. australis* and most different from *S. sarda* (Table 17). It differs from all three other species in having fewer anal fin rays (12-15, modally 14 vs. 14-17, modally 15)

and fewer total anal elements (18-22, modally 20 vs. 19-23, modally 21 or 22). *Sarda chiliensis* also has the greatest number of palatine teeth (9-22 vs. 7-14 in *S. australis*, 8-21 in *S. sarda* and *S. orientalis*) and the widest supramaxillary (slightly wider than in *S. sarda* and *S. australis*, much wider than in *S. orientalis*). *Sarda chiliensis* resembles *S. orientalis* and differs from *S. sarda* and *S. australis* in always lacking teeth on the vomer; *S. chiliensis* and *S. australis* both have a short hyomandibular spine that does not project beyond the condyle.

Morphometrically (Tables 1, 19), *Sarda chiliensis* has the shortest maxilla (463-489 thousandths of head length in the southeast Pacific population, 460-503 in the northeast Pacific), much shorter than *S. australis* (503-539) and *S. orientalis* (510-529) and the North American population of *S. sarda* (503-529), but overlapping with the eastern Atlantic populations of this species (497-511, 494-523). It has a shorter first dorsal base (267-314 thousandths of fork length) than *S. australis* (315-343) and differs from the northwest Pacific population of *S. orientalis* in snout-second dorsal and pelvic origin to vent distances.

TABLE 19.—Comparison of morphometric characters in two populations of *Sarda chiliensis*, northeast Pacific (*S. c. lineolata*) and southeast Pacific (*S. c. chiliensis*). First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

	Northeast Pacific			Southeast Pacific		
Character	Range	$\bar{x}$	N	Range	$\bar{x}$	N
Fork length (mm)	207-587	375	24	325-672	498	18
Fork length						
Snout — A	642-674	656	23	631-672	654	18
Snout — 2D	553-595	573	24	551-585	569	18
Snout — 1D	243-281	269	24	268-290	279	18
Snout — P_2	275-318	295	24	280-323	303	18
Snout — P_1	247-279	266	24	260-300	275	18
P_1 — P_2	106-121	112	21	105-131	118	16
Head length	248-275	263	24	259-292	272	18
Max. body depth	179-232	210	19	177-230	210	13
Max. body width	98-167	131	22	116-154	134	10
P_1 length	99-132	116	24	125-152	138	18
P_2 length	65- 87	78	24	65- 91	84	18
P_2 insertion - vent	329-367	353	24	327-368	346	16
P_2 tip - vent	248-331	276	24	237-352	269	17
Base 1D	278-314	297	24	267-303	286	16
Height 2D	64- 98	83	23	82-116	97	17
Base 2D	71-115	93	23	80-109	94	18
Height anal	58- 89	74	23	77-107	92	18
Base anal	61- 84	71	24	61- 88	74	18
Caudal spread	196-300	234	20	228-289	258	11
Snout (fleshy)	87-119	94	24	86-102	95	18
Snout (bony)	71- 83	78	24	75- 89	81	18
Maxilla length	115-136	126	24	121-143	130	18
Post orbital	125-144	139	21	131-150	142	16
Orbit (fleshy)	25- 44	31	24	27- 36	31	18
Orbit (bony)	47- 63	57	22	47- 63	56	18
Interorbital width	57- 69	63	24	62- 82	70	18
Head length						
Snout (fleshy)	338-368	353	23	331-363	348	18
Snout (bony)	283-308	297	24	279-329	299	18
Maxilla length	460-503	481	24	463-489	477	18
Post orbital	499-548	526	21	504-544	523	16
Orbit (fleshy)	102-168	119	24	102-141	115	18
Orbit (bony)	190-238	218	22	174-229	205	18
Interorbital width	213-278	239	24	233-302	257	18

Types of Nominal Species.—*Pelamys chiliensis* Cuvier in Cuvier and Valenciennes 1831:163. Holotype: MNHN A.5608; 672 mm FL; Chile, Valparaiso; d'Orbigny. Type previously considered by Bauchot and Blanc (1961), Blanc and Bauchot (1964, photograph-fig. 21), and Collette (1966). Counts: dorsal fin rays XVIII + 14 + VIII; anal fin rays 12 + VI; pectoral fin rays 24; gill rakers missing; upper jaw teeth 23; lower jaw teeth (left-right) 16-19.

Pelamys lineolata Girard 1859:106. Holotype: USNM 688; 266 mm FL; California, San Diego; A. Cassidy. Counts: dorsal fin rays XIX + 14 + VIII; anal fin rays 12 + VII; pectoral fin rays (left-right) 26-26; gill rakers 9 + 1 + 17 = 27; upper jaw teeth (left-right) 23-22; lower jaw teeth 18-19; palatine teeth 18-17; vertebrae 24 + 21 = 45; lamellae in nasal rosette 26.

Sarda stockii David 1943:31-33, pl. 4. Holotype: LACM 1035/1059A; originally Calif. Inst. Technol. 10039; ca. 522 mm FL; California, Santa Monica Mountains, quarry near Mulholland Drive, locality 1035; Modelo Formation; Upper Miocene. Counts from holotype: dorsal fin rays XVIII or XIX + 13 or 14 + VI; anal fin rays 12 + VI; vertebrae 24 or 25 + 21-22 = 45 or 46. Caudal rays cover the hypural plate; teeth not visible; lower jaw with anteroventral notch similar to *Sarda*.

Distribution.—*Sarda chiliensis* is restricted to the eastern Pacific Ocean. Its range is divided into north and south temperate populations by a tropical population of *S. orientalis* (Figure 70). The southern *S. chiliensis chiliensis* was originally described from Valparaiso, Chile, and has been reported as far south as Talcahuano by Buen (1958) and Valdivia at lat. 39°48'S, long. 79°13'W by Kuo (1970). Its northern limit is at Mancora, Peru (Ancieta 1964), at lat. 4°09'S, long. 81°01'W, immediately south of the Gulf of Guayaquil, Ecuador. Most of our material comes from near Callao, Peru.

The northern subspecies, *S. c. lineolata* was originally described by Girard (1859) from San Diego, Calif. It regularly reaches south to Magdalena Bay, Baja California (Radovich 1961; CAS

SU 61662, Blanca Bay, lat. 24°46′30″N, long. 112°15′W), and occasionally to Cabo San Lucas at the tip of Baja California (lat. 22°20′N, long. 112°27′W). There is one specimen (Ricker 1959b; UBC 57-149) from Socorro Island in the Revillagigedos Islands 250 miles south of Cabo San Lucas. It is not common north of Point Conception, Calif., but there are several scattered records: off the Farallon Islands and off Eureka, Calif. (Radovich 1961); Puget Sound (Starks 1910, Patten et al. 1965); east coast of Vancouver Island, British Columbia (Manzer 1965; UBC 64-394); and coastal Alaska (Quast 1964) in Clarence Strait northwest of Ketchikan (USNM 213494) and off the Copper River at lat. 60°16′N, long. 145°32′W (USNM 213495).

Geographic Variation.—Although the temperate northeast (*c. lineolata*) and southeast (*c. chiliensis*) Pacific populations of *Sarda chiliensis* are completely separated from each other by the tropical eastern Pacific population of *S. orientalis* (Figure 70), there are few differences between the two populations; anatomically they are virtually identical. The caecal mass extends posteriorly for more than half the length of the body cavity in ventral view in the northeast population; less than half this distance in the southeast population.

Walford (1936) used the posterior extent of the corselet to distinguish the northeast *Sarda lineolata* (pectoral fin extends scarcely beyond corselet) from the southeast *S. chiliensis* (pectoral fin extends an eye diameter further). Hildebrand (1946) considered this character entirely unreliable in separating the two populations. Kuo (1970) measured the extent of the corselet in 380 specimens from southern California and 49 from Callao, Peru. He found that the corselet does extend further posteriorly in the southern population but that the interpopulational differences were not significant at the 5% level. He concluded that the character was not reliable even for subspecific separation of the two populations.

Morphometrically, there are some differences in the ranges and means between the two populations (Table 19), but these are smaller than those between some populations of *S. sarda* and *S. orientalis*. Kuo (1970) found, through covariance analyses and scatter diagrams, significant differences at the 1% level between the two populations in such morphometric characters as head length, predorsal length, prepelvic length, and the distance from the origin of the second dorsal and anal fins to the caudal base.

Among meristic characters, the total number of vertebrae is the best distinguishing character between the southeast and northeast populations of *Sarda chiliensis*. The northeast population has more vertebrae (Table 9) with means of 44.9 for our data, 44.8 for Kuo (1970), and 45 ± 0.47 for a sample of 19 reported by Vildoso (1963b). Our data for 23 southeast specimens ($\bar{x}$ 44.2) agrees with that reported by Vildoso (1963b) for two samples, 44.15 ± 0.40 for 38 specimens, and 44.21 ± 0.40 for a sample of 100. Kuo (1970), however, found even fewer: a range of 42-46 with a mode of 43 and a mean of 43.4 compared to our range of 43-46, mode 44, mean 44.2. The reasons for the discrepancies between our data and that of Vildoso on the one hand, and that of Kuo on the other are not known. We have reexamined seven of Kuo's southeastern specimens and find totals of 43 (1 specimen), 44 (5), and 45 (1).

There are also differences in the highly variable number of teeth in the upper and lower jaws (Tables 5, 6) with the northeast Pacific population having slightly more: upper jaw 20-30, $\bar{x}$ 23.7 vs. 18-28, $\bar{x}$ 23.0; lower jaw 15-25, $\bar{x}$ 19.4 vs. 14-23, $\bar{x}$ 18.9.

The available data does not convince us that the northeast and southeast Pacific populations are subspecies. However, as the populations are genetically isolated from each other and there are some significant differences, there is practical value in using the available subspecific names, and there is ample historical precedent for the name *lineolata* for the northeast population. Therefore, we have emphasized comparisons between the two geographic populations by labelling the populations northeast and southeast Pacific in the tables but have retained the subspecies designations in the formal synonomies.

Sarda orientalis (Temminck and Schlegel)
Indo-West Pacific

Pelamys orientalis Temminck and Schlegel 1844:99 (original description, Japan), pl. 52. Richardson 1846:268 (Sea of Japan). Günther 1860:368 (description). Tirant 1885:46 (Cambodia).

Pelamys chilensis (not of Cuvier 1831). Day 1878:253-254 (description; Bombay), pl. 56, fig. 1.

Sarda chilensis var. *orientalis*. Steindachner and Döderlein 1884:179 (description; Japan).

Sarda orientalis. Jordan and Snyder 1900:352 (Tokyo). Jordan and Snyder 1901:64 (Tokyo, Nagasaki). Kishinouye 1923:424-426 (description, anatomy; Japan, southern species abundant around Kyushu, juvenile from Aomori, Honshu), figs. 11, 17, 33, 42. Jordan and Hubbs 1925:215 (not uncommon in Japanese markets). Walford 1936:9 (*S. orientalis* separate species from *S. velox*). Tortonese 1939:323-324 (Yokohama, Japan). Boeseman 1947:94-95 (lectotype of *P. orientalis* selected). Smith 1949:299 (description; south to Durban, South Africa). Warfel 1950:18 (description; Philippine Islands), 21 (fig. 14, fish, gill arch, excised liver). Fraser-Brunner 1950:147-148 (description), fig. 12. Honma 1952:143 (Echigo Province, Honshu, Japan). Herre 1953:251 (Philippine Islands). Morice 1953a:37-39 (dentition; number of gill rakers and vertebrae), fig. 5 (after Warfel 1950). Godsil 1955:22-35, figs. 7-13, tables 4-6 (description, anatomy, five Japanese specimens). Smith 1956:721 (Aldabra). Munro 1958a:113 (Western Australia), fig. 755. Jones 1961:343,346, fig. 10 (158 mm. juvenile, fig. 11 (80 mm juvenile). Jones and Silas 1961:379-380 (Vizhingam and Cape Comorin, Western India), fig. 6 (juvenile and adult). Collette and Gibbs 1963b:30 (Indian Ocean), pl. 9, upper fig. Jones and Silas 1963:1787 (distribution in Indian Ocean). Kikawa et al. 1963:147-156 (species synopsis). Thomas and Kumaran 1963:1667 (diet in Indian waters mostly fish). Boeseman 1964:465, pl. 3, fig. 11 (lectotype of *P. orientalis*). Jones and Kumaran 1964:357-358, 360, fig. 60 (after Jones 1961). Jones and Silas 1964:26 (description), pl. 8A. Kumaran 1964:605 (diet 98% fish). Rao 1964:736 (ripe ovaries). Nakamura and Kikawa 1966:60-62 (infracentral grooves on vertebrae). Sivasubramaniam 1967:29 (catch in Ceylon), 44 (fig. 14, length-weight). Gnanamuttu 1968:365 (Madras). Sivasubramaniam 1969:73-77 (description, biology; Ceylon), pl. 1 (photos of juvenile and adult). Nair et al 1970:13-17 (biology, description; India). Nagabhushanam and Chandrasekhara Rao 1972:303 (Minicoy Atoll, Laccadive Archipelago).

Sarda chilensis (not of Cuvier 1831). Jordan and Snyder 1904:125 (description; Honolulu). Jordan et al. 1913:121 (Japan). Jordan and Jordan 1922:32 (occasional at Hawaii). Barnard 1927:801 (description; Natal coast, South Africa). Fowler 1928:134-135 (Hawaii). Chevey 1934:45-46 (Tirant's Cambodia record). Tinker 1944:160-161 (Hawaii). Brock 1949:275 (in key to Hawaiian scombrids).

Sarda chiliensis (not of Cuvier 1831). Fowler 1938:277 (Honolulu). Fowler 1949:73 (Honolulu).

Sarda orientalis serventyi Whitley 1945:41 (original description; Western Australia). Whitley 1947:146, pl. 11, fig. 4 (holotype). Whitley 1948:24 (range in Western Australia). Whitley 1964a:236, 242 (Western Australia). Whitley 1964b:48 (listed).

Sarda orientalis
Eastern Pacific

Sarda chilensis (not of Cuvier 1831). Gilbert and Starks 1904:68 (description; Panama City).

Sarda chiliensis (not of Cuvier 1831). Herre 1936:107 (Galapagos). Erdman 1971:68-69 (Gulf of Nicoya, Costa Rica).

Sarda velox Meek and Hildebrand 1923:320-321 (original description; Panama City), pl. 24. Walford 1936:8-10 (description; recognized as valid species). Walford 1937:23 (description), col. pl. 38a. Schmitt and Schultz 1940:3 (Galapagos Islands [USNM 107055]). Fowler 1944:342 (Galapagos Islands [ANSP 82007, 89065]). Hildebrand 1946:374-375 (description; Gulf of Guayaquil, Peru [USNM 127907]; Galapagos; Pearl Islands, Panama). La Monte 1952:44, 46 (description), pl. 15. Morice 1953a:37 (listed). Godsil 1954:44-59 (description; anatomy; 4 Galapagos specimens), tables 6, 7 (counts and measurements), figs. 21-27 (morphometrics), figs. 28-33 (anatomy), figs. 35-41 (osteology). Vildoso 1963b:1549-1556 (description; range). Laevastu and Rosa 1963:1844 (fig. 7, distribution map).

Sarda orientalis. Fraser-Brunner 1950:147 (*S. velox* a synonym of *S. orientalis*). de Sylva 1955:38, fig. 61 H (dorsal view of skull). Godsil 1955:36-42 (no significant anatomical differences between *S. velox* and *S. orientalis*). Ricker 1959a:13 (S. Baja California; Las Tres Marías Islands). Silas 1964:296 (in part; in key and on range map). Fitch and Craig 1964:202 (sagittae of three species of *Sarda* almost identical).

Comparative Diagnosis.—*Sarda orientalis* is similar to *S. australis* and *S. chiliensis* in an equal

number of characters (Table 17). It differs from the other species of *Sarda* in having the lowest number of gill rakers (8-13 vs. 16-27); a very narrow supramaxillary; the dorsal projection of the ectopterygoid slightly expanded versus pointed; only a trace of a depression in the position of the elliptical ceratohyal window; no depression on the ventral surface of the proximal portion of the glossohyal; the haemal postzygapophyses of the last precaudal vertebra and the haemal prezygapophyses of the first caudal vertebra abutting against each other; gall bladder not visible in ventral view between the intestine and spleen; and a narrower and longer vertical wing to the pelvic girdle. *Sarda orientalis* is similar to *S. sarda* in having a long hyomandibular spine that projects beyond the condyle and in having a low number of palatine teeth (8-19 vs. 8-21). *Sarda orientalis* is sharply differentiated from *S. chiliensis* in having fewer gill rakers, a much narrower supramaxillary, and also in having fewer larger teeth (upper jaw 12-20, $\bar{x}$ 15.5 vs. 18-30, $\bar{x}$ 23.5; lower jaw 10-17, $\bar{x}$ 13.0 vs. 14-25, $\bar{x}$ 19.2).

Morphometrically (Tables 1, 20), *Sarda orientalis* is generally similar to the other species of *Sarda*. It does have a longer maxilla (141-149 and 146-156 thousandths of fork length in the northwest and eastern Pacific populations, respectively) than *S. chiliensis* (115-143) and *S. sarda* (125-145). The base of the first dorsal fin (285-327, 282-302) is shorter than that of *S. australis* (315-343).

TABLE 20.–Comparison of morphometric characters in populations of *Sarda orientalis* from Japan and the eastern tropical Pacific. First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

Character	Japan			East tropical Pacific		
	Range	$\bar{x}$	*N*	Range	$\bar{x}$	*N*
Fork length (mm)	342-560	432	7	354-613	472	10
Fork length						
Snout — A	674-703	694	5	662-703	678	10
Snout — 2D	596-614	606	5	569-596	582	10
Snout — 1D	273-308	286	7	274-311	288	10
Snout — P_2	293-316	303	5	299-321	310	10
Snout — P_1	272-292	281	7	277-299	290	10
P_1 — P_2	109-118	113	5	105-118	114	10
Head length	268-286	278	7	266-294	284	10
Max. body depth	221-244	234	4	193-236	213	10
Max. body width	143-151	146	4	127-153	144	10
P_1 length	104-125	115	7	119-134	127	10
P_2 length	70- 78	76	5	81- 91	86	10
P_2 insertion - vent	374-419	392	7	353-384	367	10
P_2 tip - vent	305-322	311	3	265-302	280	10
Base 1D	285-327	306	7	282-302	292	10
Height 2D	75- 82	78	7	89-101	94	8
Base 2D	85-111	93	7	88-107	95	9
Height anal	61- 85	73	7	84- 97	89	8
Base anal	66- 78	73	7	73- 83	79	9
Caudal spread	168-234	214	4	192-259	236	5
Snout (fleshy)	86-103	96	7	98-105	101	10
Snout (bony)	80- 97	86	7	83- 91	86	10
Maxilla length	141-149	145	6	146-156	150	10
Post orbital	128-147	139	5	141-151	146	10
Orbit (fleshy)	32- 60	42	7	34- 40	37	10
Orbit (bony)	29- 65	56	7	60- 68	64	10
Interorbital width	67- 73	71	6	65- 79	71	10
Head length						
Snout (fleshy)	306-368	344	7	348-369	357	10
Snout (bony)	288-344	308	7	291-317	303	10
Maxilla length	510-529	522	6	512-557	528	10
Post orbital	476-525	503	5	494-553	512	10
Orbit (fleshy)	102-152	136	7	120-147	130	10
Orbit (bony)	210-234	220	7	210-238	226	10
Interorbital width	251-263	256	6	230-283	251	10

Types of Nominal Species.–*Pelamys orientalis* Temminck and Schlegel 1844:99, pl. 52. There are three syntypes in Leiden of which Boeseman (1947:94-95; 1964:465, pl. 3, fig. 11) selected the largest as lectotype. Lectotype: RMNH 2286; about 560 mm FL, stuffed and mounted; Japan; 1830; Burger. Paralectotypes: RMNH 842; about 470 mm, stuffed and mounted; Japan; Burger. RMNH 1244; 451 mm, stuffed but preserved in alcohol; Japan; 1824-29. Counts for lectotype (paralectotypes in parentheses): dorsal fin rays XVIII+14+VIII (XVIII+14+VIII, XIX+15+VIII); anal fin rays ca. 14+VI (ca. 13+VI, 15+VI); pectoral fin rays 24 (23-23, 25-24); gills missing in all three; upper jaw teeth ca. 14 (ca. 13-11, 15-17); lower jaw teeth (left-right) 12-12 (?, 12-13).

Sarda velox Meek and Hildebrand 1923:320-321, pl. 24. Holotype: USNM 81060; 364 mm FL; Panama City market; 19 Jan. 1912; S. E. Meek and S. F. Hildebrand. Counts: dorsal fin rays XVIII+15+VIII; anal fin rays 15+VI; pectoral fin rays (left-right) 25-24; gill rakers 3+1+8=12; upper jaw teeth (left-right) 17-19; lower jaw teeth 13-11; vertebrae 25+20=45; lamellae in nasal rosette 34-32.

Sarda orientalis serventyi Whitley 1945:41. Holotype figured in Whitley (1947:pl. 11, fig. 4). Holotype: WAM P.3512; 265 mm FL; Western Australia, Perth. Paratype: WAM P.2568; 480 mm; Western Australia, Busselton. The holotype could not be located when Collette visited Perth in 1970. Counts for paratype: dorsal fin rays XVIII+14+VIII; anal fin rays 14+VI; pectoral fin rays 24-24; no gills; upper jaw teeth (left-right) 19-17; lower jaw teeth 15-14; palatine teeth 13.

Distribution.–*Sarda orientalis* is widespread in the Indo-Pacific but there are two reports from the Atlantic Ocean. Nichols and Breder (1927) record-

ed it (as *S. velox*) from Block Island, R.I., based on a drawing (Stillman 1921). We do not believe a positive identification of a species of *Sarda* can be based solely on a drawing. Fraser-Brunner (1950) "confirmed" the presence of *S. orientalis* in the Atlantic based on a specimen from the Gold Coast (Ghana), but reexamination of this specimen (BMNH 1939.7.12.31) shows it to be a perfectly normal *S. sarda*.

There appear to be large gaps between populations in the tropical Indo-West Pacific (Figure 70). In the western Indian Ocean, it is recorded from along the coast of Natal, South Africa (Barnard 1927; ANSP 91185), south to Durban (Smith 1949; BMNH 1920.7.23.59). It occurs at Aldabra (Smith 1956) and in the Seychelles Islands (Smith and Smith 1963; BMNH 1927.4.14.81). We have examined specimens from Eilat at the northern end of the Gulf of Aqaba in the Red Sea (SFRS 704/1-2) and from Muscat at the entrance to the Persian Gulf (BMNH 1888.12.129-131). Day (1878) gave an early report from Bombay. Silas (1964, fig. 7) mapped the occurrence and fishery areas for *Sarda orientalis* in the eastern Arabian Sea along the southwest coast of India and Nagabhushanam and Chandrasekhara Rao (1972) listed it among the fauna of Minicoy Atoll, Laccadive Archipelago. Sivasubramaniam (1967, 1969, 1970) recorded it as one of the least abundant tunas in the inshore water of Sri Lanka (Ceylon); we have examined a juvenile from there (UBC 57-183). Small quantities were taken in gill nets off Madras in 1966 (Gnanamuttu 1968). We have not seen any records or specimens from the eastern Indian Ocean except for the southwest tip of Australia from where Whitley (1945) described *S. orientalis serventyi* (Albany and Busselton, Western Australia; WAM P. 2568).

There appear to be no records or museum specimens of *Sarda orientalis* from Indonesia or elsewhere in the East Indies. There is an old published record for Cambodia (Tirant 1885), but we have seen no specimens from the Gulf of Thailand or South China Sea in any collections including the extensive series of scombrids collected by the George Vanderbilt Expedition. Warfel (1950) and Herre (1953) reported it from the Philippine Islands and there are specimens from Shanghai (MNHN 91-628; NHMV uncat.). Starting with its original description by Temminck and Schlegel in 1844, there have been numerous reports from Japan where it is not uncommon in many markets (Jordan and Hubbs 1925): Richardson 1846 (Sea of Japan); Jordan and Snyder 1900 (Tokyo); Jordan and Snyder 1901 (Tokyo and Nagasaki); Tortonese 1939 (Yokohama). Kishinouye (1923) reported *S. orientalis* as abundant around the island of Kyushu and he recorded a juvenile from north as far as Aomori Prefecture (about lat. 41°N) at the north end of Honshu. According to Kikawa et al. (1963), this remains the northernmost record of the species in Japan. Honma (1952) listed it from Sado Island (about lat. 38°N), Niigata Prefecture, in the Sea of Japan. Carl L. Hubbs obtained specimens (UMMZ uncat.) from Suruga Bay and Sagami Bay in 1923 and Collette purchased specimens in the Tokyo market in 1966. There appears to be a large gap in the range from Japan and China on the north and the Philippine Islands further south all the way east to the Hawaiian Islands where it is not common (Jordan and Snyder 1904; Jordan and Jordan 1922; Fowler 1928; Tinker 1944; Brock 1949); however, we have examined two preserved Hawaiian specimens (USNM 58527; ANSP 82258) and have dissected two recently collected specimens.

The eastern Pacific population is confined to the tropical coasts of Middle America and Ecuador and also occurs in the Galapagos Islands. This population was described as *Sarda velox* by Meek and Hildebrand in 1923 from Panama City specimens and several other records are also from Panama and the Pearl Islands (Gilbert and Starks 1904; Hildebrand 1946; CAS SU 12824; USNM 81060, 128643-5). The range extends south to the Galapagos (Herre 1936; Schmitt and Schultz 1940; Fowler 1944; Hildebrand 1946; Godsil 1954; ANSP 82007, 89065; CAS SU 4885; USNM 107055, 119781) and the Gulf of Guayaquil, Ecuador (Hildebrand 1946; USNM 127907). To the north, there are records from the Gulf of Nicoya, Costa Rica (Erdman 1971) and from the coast of Mexico at Banderas Bay, Las Tres Marías Islands, and Cape San Lucas (NMC 68-0710) at the southern tip of Baja California (Ricker 1959a).

Geographic Variation.—The distribution of *Sarda orientalis* (Figure 70) is disjunct and, therefore, subspecific or populational differences are possible. Two forms have been named—the population in southwestern Australia (*S. orientalis serventyi* Whitley) and the tropical eastern Pacific population (*S. velox* Meek and Hildebrand). Based on the scattered material available, there appear to be no significant anatomical or meristic

differences between any populations of the species. Morphometrically, there appear to be some differences between the small samples from Japan and the eastern Pacific (Table 20), in such characters as snout-second dorsal distance, pelvic fin tip to vent, height of anal and second dorsal fins. Until more material is examined, there does not seem to be adequate data to support recognition of subspecies in *S. orientalis*. However, to facilitate entry into the literature, the synonomies have been divided into Indo-West Pacific (including Hawaii) and tropical eastern Pacific.

Sarda sarda (Bloch)

Pelamis Belon 1553:177-179 (description).

Amia Rondelet 1554:238-241 (description, fig.).

Pelamyde vera Rondelet 1554:245-248 (description, fig.)

Pelamyde sarda Rondelet 1554:248 (description, fig.).

Thunnus authoris primus Aldrovandi 1613:313 (fig.).

Pelamys sarda Willughby 1686:179 (description).

Scomber pelamis Brünnich 1768:68-69 (original description; Adriatic Sea; preoccupied by *Scomber pelamis* Linnaeus, 1758 [= *Katsuwonus pelamis*]).

Bonite Duhamel du Monceau 1769: pl. 7, fig. 2.

Thonin sorte de pélamide Duhamel du Monceau 1769: pl. 7, fig. 5.

Scomber sarda Bloch 1793:44-48 (original description; pre-Linnean synonymy; Europe) pl. 334. Bloch and Schneider 1801:22-23 (description; Mediterranean and Atlantic). Risso 1810:168-169 (description; Nice).

Scomber mediterraneus Bloch and Schneider 1801:23 (substitute name for *Scomber pelamis* Brünnich; description). Delaroche 1809:336 (description; Balearic Islands and Mediterranean coast of Spain).

Scomber palamitus Rafinesque 1810:44-45 (original description; Palermo, Sicily), pl. II, fig. 2.

Scomber ponticus Pallas 1811:217 (original description; Crimea).

Thynnus pelamis. Risso 1826:415-416 (synonymy; description; Nice).

Thynnus sardus. Risso 1826:417 (synonymy; description; Nice).

Thynnus brachypterus Cuvier 1829:198 (original description based on the *pelamyde vera* of Rondelet (1554:245) and the thonin sorte de pélamide of Duhamel du Monceau (1769:pl. 7, fig. 5).

Sarda sarda. Cuvier 1829:199 (original description of *Sarda*). Dresslar and Fesler 1889:440-441 (synonymy; description; Woods Hole, Mass.), pl. 8. Berg 1895:41 (Mar del Plata, Argentina). Jordan and Evermann 1896:872 (description; synonymy). Ihering 1897:52 (Rio Grande do Sul, Brazil). Fowler 1915:532 (Trinidad). Miranda Ribeiro 1918:766 (Santos, Brazil). Schroeder 1924:6 (uncommon in Florida Keys). Chabanaud 1925:199-200 (vertebral number; West Africa), fig. (dentition). Fowler 1926:268 (Buenos Aires). Barnard 1927:800 (description; Cape Seas, South Africa). Chabanaud and Monod 1927:279 (Port Étienne, Mauritania). Nichols and Breder 1927:122-123 (description; Western Atlantic north to Casco Bay, Maine) fig. 169. Buen 1930a:40 (pl. 1, fig. 4), 46 (synonymy; description; Spain). Buen 1930b:1-32 (larvae and juveniles; Mediterranean Sea), figs. Dieuzeide 1930:134-140 (synonymy; description; Algeria), pl. 2. Le Gall 1934b:287 (description), fig. (after Smitt). Pozzi and Bordale 1935:162 (lat. 35-38°S, Argentina). Vladykov 1935:7-8 (Nova Scotia). Fowler 1936:626-627 (synonymy; description; Italian and New Jersey specimens). Walford 1936:9 (key to species of *Sarda*). Cadenat 1937:482 (Cape Verde, Sénégal). Lovén 1938:274-280 (Scandinavian records), 275 (fig. 1), 276 (fig. 2, map). McKenzie 1939:16 (St. Margaret's Bay, Nova Scotia). Baughman 1941:18 (Texas [USNM 118644-6]). Jensen 1941:201-202 (14 locality records from the Kattegat off Denmark). Redeke 1941:212-213 (description; Netherlands). Chabanaud 1944:3-6 (*S. sarda* a distinct species). La Monte 1945:20-21, col. pl. 8. Irvine 1947:185-186 (description; Accra, Ghana). Poll 1947:284-285 (description), fig. 183. Molteno 1948:23 (abundant off Angola and South West Africa; summer schools from Cape Point to Mosselbaai, South Africa). Smith 1949:299 (occasional at Cape Point, South Africa), col. pl. 66, fig. 833. Tortonese and Trotti 1949:86 (common in Ligurian Sea). Cadenat 1950:134 (Cape Verde Islands). Fraser-Brunner 1950:146-147 (key; range), fig. 11. Postel 1950:59-62 (description; length-frequency; biology; Cape Verde Islands). Rivas 1951:223 (synonymy; description; Western Atlantic). La Monte 1952:46 (description; range), col. pl.

17. Lozano y Rey 1952:523-527 (synonymy; description), col. pl. 39, fig. 4. Bigelow and Schroeder 1953:337-338 (description; habits; range in Gulf of Maine), fig. 180 (after Smitt). Morice 1953a:37-41 (anatomy), p. 58 (fig. 5 after Dresslar and Fesler 1889). Morice 1953b:72 (fig. 6, liver). Belloc 1954:297-310 (description; synonymy; Mediterranean distribution; biology; fishery). Collins 1954:27 (Azores). Mather and Day 1954:182 (Spanish Sahara). Pew 1954:28-30 (Texas), fig. 27. Postel 1954:357-358 (stomach contents); 359 (parasites), 361 (gonosomatic index). Dieuzeide et al. 1955:147-148 (description; range; fig.; Algeria). Dollfus 1955:55 (listed), 141 (references; Atlantic coast of Morocco). Frade and Postel 1955:34 (gonads; spawning season; Cape Verde Islands), 35 (fig. 5, ovary). Hildebrand 1955:206 (common sports fish in northwest Gulf of Mexico; 6 trawled west of Campeche). Nümann 1955:75-127 (migrations in the Black Sea and Sea of Marmara). A. Postel 1955:57-67 (number of teeth in 503 specimens; Tunisia). E. Postel 1955a:1-167 (summary of biology in the tropical eastern Atlantic). E. Postel 1955b:31-32 (sex ratio; maximum size). Springer and Bullis 1956:71 (Arcas Cay, off Campeche, Mexico). Mather and Gibbs 1957:243 (Shag Harbour, Nova Scotia). Ionescu et al. 1958:165-186 (biology; Roumania). Klawe and Shimada 1959:111 (2 juveniles, 64-67 mm; Gulf of Mexico), 112 (fig. 6, 67-mm juvenile). Gordon 1960:47-48 (summer visitor to Block Island Sound, R.I. Bauzá Rullán 1961:155-156 (otoliths), pl. 1 (figs. 7-10, sagittae). Klawe 1961a:154 (34-mm juvenile off Charleston, S.C.). Mansueti 1962:47-49 (description; Chesapeake Bay). Nunes-Ruivo 1962:17 (copepod *Caligus pelamydis* from Angolan specimen). Collette and Gibbs 1963a:26 (species of *Sarda*). Demir 1963:101-129 (description, synonymy; range; biology, especially in the Black Sea). Idyll and de Sylva 1963:755-760 (biology; western Atlantic). Laevastu and Rosa 1963:1844 (fig. 7, map of distribution and fishing areas). Bănărescu 1964:805-809 (synonymy; description; ecology; Roumania), fig. 355 (adult), fig. 356 (larvae). Demir 1964:455-457 (meristics of 1,000 specimens; Black Sea and Sea of Marmara). Fitch and Craig 1964:202 (sagittae of three species of *Sarda* almost identical). George et al. 1964:21 (Lebanon, rare). Postel 1964:220 (summary of biology, North Africa). Svetovidov 1964:389-395 (extensive synonymy; description; biology; Black Sea), fig. 125 (adult), fig. 126 (juvenile). Boschung 1966:227-228 (Gulf of Mexico records; stomach contents). Rodrígues-Roda 1966:269-279 (biology; Spanish trap net fishery 1958-1964). Jensen 1967:45-46 (central and western Gulf of Guinea). Padoa 1967:479-483 (eggs and larvae), figs. 308-312 (eggs and larvae). Bini 1968:37-38 (description; col. fig.). Granier 1968:325 (Golfe d'Aigues-Mortes, Golfe du Lion, France). Rae and Pirie 1968:212 (Montrose, east coast of Scotland). Went 1968:37-38 (Streedagh, near Grange, County of Sligo, Ireland; previous Irish records). Williams 1968:436 (Gulf of Guinea). Dornescu and Mişcalencu 1968:15 (perciform type of branchial apparatus). Muir 1969:168 (gill dimensions). Rae and Pirie 1969:279 (Garliestoń, Scotland). Went 1969:149 (7 previous Irish records). Wheeler and Blacker 1969:327 (British seas 1966-67). Lozano Cabo 1970:158 (Spanish Morocco). Mago Leccia 1970:109 (Venezuela). Muir 1970:22 (measurements of branchial vessels of second gill arch). Carey et al. 1971:136 (body temperature). Dahl 1971:276-277 (Colombia). De Groot and Nijssen 1971:8 (Arguin Bank, Mauritania). Went 1971:44 (Irish records). Adamicka 1972:308-331 (functional anatomy of the head), figs. 1-4 (head muscles). Wheeler and Blacker 1972:162 (British seas, 1968-69). Postel 1973:475 (synonymy; distribution).

Pelamys sarda. Cuvier in Cuvier and Valenciennes 1831:149-162 (synonymy; description; Cape Verde Islands and Brazil); pl. 217. Rathke 1837:335 (*Scomber ponticus* Pallas a synonym of *P. sarda*). Bonaparte 1845:74 (synonymy). Guichenot 1850:58 (synonymy; Algeria). Lowe 1850:248 (Madeira). Storer 1855:141-143 (description; Massachusetts), pl. 11, fig. 5. Günther 1860:367 (synonymy; description). Duméril 1858:262 (Cape Verde Islands). Steindachner 1865:401 (Canary Islands). Steindachner 1868:358-360 (description; Iberian Peninsula and Canary Islands). Canestrini 1870:103 (description; Italy). Collett 1879a:19-20 (description; Christiana (= Oslo), Norway). Giglioli 1880:25 (Italy). Moreau 1881:430-434 (synonymy; description; France). Ninni 1882:264 (Adriatic). Rochebrune 1882:95

(Cap Vert). Hilgendorf 1888:208 (Azores Islands). Osorio 1890:56 (Angola). Vinciguerra 1893:93 (Canary Islands). Griffini 1903:398 (description; Italy). Pellegrin 1908:89-90 (Dakar), fig. 6. Shepherd 1910a:59, fig. 13 (asteriscus). Shepherd 1910b:293, fig. 1 (sagitta). Parona 1919:84-91 (synonymy; common names; description; distribution; Italy; col. pl. 8). Farran 1923:106 (Ireland). Sanzo 1932:3-9 (eggs and larvae; Italy; col. pl. with 7 figs. of egg and developing embryo). Athanassopoulos 1934:315-316 (Greece; Sea of Marmora). Liebman 1934:325 (Israel).

Palamita sarda. Bonaparte 1831:173 (original description of *Palamita*, substitute name for *Pelamys* Cuvier, preoccupied).

Pelamis sarda. Valenciennes 1844:49-50 (Canary Islands). Verany 1847:493 (Liguria, Italy). Ehrenbaum 1924:10-11 (vertebral counts; description of 7.2-mm larva from Oran, Algeria); fig. 3a (7.2-mm larva) and 3b (preopercle of larva).

Sarda pelamys. Gill 1862:126 (type-species of *Sarda*). Jones 1879:88 (Halifax, Nova Scotia).

Sarda mediterranea. Jordan and Gilbert 1882:427-428 (description; both sides of Atlantic; synonymy). Carus 1893:659 (Mediterranean). Šoljan 1963:147 (description; figs.; Adriatic Sea).

Sarda pelamis. Smitt 1892:105-107 (synonymy; description; occasional visitor to Scandinavia), fig. 30. Sanz Echeverría 1926:150 (sagitta). Jensen 1937:10-11 (a summer visitor to the Skagerak and Kattegat). Otterstrøm 1943:125-126 (summary of previous records from Denmark, photograph).

Comparative Diagnosis.–*Sarda sarda* is the most distinct species in the genus and can be distinguished from the other three species by higher counts in several characters (Table 17). Dorsal spines number 20-23 compared to 17-19; vertebrae 50-55 vs. 43-46; pleural ribs 24 vs. 19-23; intermuscular bones 31-45 vs. 32-36; keels on vertebrae number 5-10 (counting from hypural plate anteriorly) vs. 5-8. *Sarda sarda* is closest to *S. australis* in several characters: numbers of anal rays, gill rakers, upper and lower jaw teeth, occasional presence of vomerine teeth, angle of the hyomandibular spine and the condyle, width of the supramaxilla, and relative length of the haemal pre- and postzygapophyses on the first caudal vertebra. As in *S. australis*, the supramaxilla is intermediate in width, wider than in *S. orientalis*, but narrower than in *S. chiliensis*. *Sarda sarda* resembles *S. orientalis* in having a long hyomandibular spine, projecting beyond the condyle.

Morphometrically (Tables 1, 21), *Sarda sarda* is similar to the other species of *Sarda* but has a shorter first dorsal base (291-330 thousandths of fork length, $\bar{x}$ 311 vs. 315-343, $\bar{x}$ 326) and smaller orbit (35-64 vs. 60-80, $\bar{x}$ 66) than *S. australis*. The first dorsal fin base is longer than in *S. chiliensis* (329-368) as is also the maxilla (494-529 thousandths of head length vs. 463-503). *Sarda sarda* differs from *S. orientalis* in averaging a longer head and greater distances from snout to anal origin and snout to pelvic fin origin.

Types of Nominal Species.–*Scomber pelamis* Brünnich 1768:68-69. Adriatic Sea. No types known to be extant. Counts from the original description (dorsal fin rays XXIII + 15 + VIII; anal fin rays 15 + VII; pectoral fin rays 24) leave little doubt about the description being of *S. sarda*.

Scomber sarda Bloch 1793:44-48, pl. 334. Europe. No types known to be extant. The plate leaves little doubt as to the identity of the description. Counts from the original description: dorsal fin rays XXI + 15 + VII; anal fin rays 14 + VI.

Scomber palamitus Rafinesque 1810:44-45, pl. 2, fig. 2. Palermo, Sicily. No types known to be extant. Original description states that there are 20 spines in the first dorsal fin and the figure is of *S. sarda*.

Scomber ponticus Pallas 1811:217. Black Sea. No types known to be extant. Original description includes counts of dorsal fin rays XXII + 14 + IX; anal finlets VIII; and pectoral fin rays 25.

Thynnus brachypterus Cuvier 1829:198. The original description is not based on specimens but on pre-Linnean authors–the "pelamyde vera" of Rondelet (1554:245-248) and the "thonin sorte de pélamide" of Duhamel du Monceau (1769:pl. 7, fig. 5). The large teeth, general body shape, and broad vertical bands show both figures to be of juvenile *Sarda*. The specimens used by Cuvier (in Cuvier and Valenciennes 1831) in the redescription of *T. brachypterus* and considered by Bauchot and Blanc (1961) and Blanc and Bauchot (1964) as types are not types. (As Collette 1966, pointed out, four of these specimens are *Thunnus thynnus* and one is *Euthynnus alletteratus*).

Distribution.–*Sarda sarda* occurs along the tropical and temperate coasts of the Atlantic

TABLE 21.–Comparison of morphometric characters in populations of *Sarda sarda* from North America, the Mediterranean Sea, and the Gulf of Guinea. First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

	North America			Mediterranean			Gulf of Guinea		
Character	Range	$\bar{x}$	N	Range	$\bar{x}$	N	Range	$\bar{x}$	N
Fork length (mm)	228-500	362	17	260-504	376	7	305-443	379	9
Fork length									
Snout — A	646-690	668	13	641-685	660	7	648-666	657	9
Snout — 2D	570-594	582	13	563-593	579	7	570-585	578	9
Snout — 1D	262-275	270	13	257-284	266	7	262-306	298	9
Snout — P_2	286-304	296	12	280-302	288	6	267-284	275	9
Snout — P_1	259-284	269	13	255-274	263	7	253-273	267	9
P_1 — P_2	105-118	111	12	94-114	104	7	107-118	111	8
Head length	256-272	264	13	251-268	259	7	253-278	271	9
Max. body depth	200-224	214	8	197-216	205	5	195-228	217	8
Max. body width	96-171	135	10	115-148	131	6			
P_1 length	96-138	115	13	105-127	116	6	120-136	130	9
P_2 length	73- 84	79	12	76- 86	82	7	77- 87	83	9
P_2 insertion - vent	348-403	366	13	356-379	370	7	341-388	357	9
P_2 tip - vent	269-302	282	12	269-297	285	7	252-293	266	9
Base 1D	291-330	311	13	301-323	311	7	298-323	311	9
Height 2D	68- 90	80	10	85-117	95	5	81- 99	91	9
Base 2D	85-113	96	13	93-112	104	5	92-112	107	9
Height anal	68- 98	77	11	68- 85	79	6	77- 91	85	9
Base anal	63- 86	73	13	69- 90	78	7	66- 89	80	9
Caudal spread	204-235	222	5	226-270	247	4	223-289	253	3
Snout (fleshy)	76-100	94	13	88- 98	93	7	88-101	96	9
Snout (bony)	78- 93	82	13	74- 83	78	7	75- 85	82	9
Maxilla length	131-141	136	13	127-136	131	7	125-145	138	9
Post orbital	130-142	136	11	126-136	132	7	133-144	138	9
Orbit (fleshy)	27- 40	32	17	27- 34	31	7	31- 36	34	9
Orbit (bony)	35- 64	57	13	53- 62	57	6	53- 64	60	9
Interorbital width	59- 73	64	13	59- 64	62	7	58- 65	63	9
Head length									
Snout (fleshy)	354-374	360	17	346-367	358	7	346-366	353	9
Snout (bony)	289-342	309	13	289-312	303	7	293-308	301	9
Maxilla	503-529	514	13	497-511	505	7	494-523	509	9
Post orbital	494-541	516	11	503-521	511	7	489-519	506	9
Orbit (fleshy)	100-149	121	17	104-133	118	7	116-132	122	9
Orbit (bony)	203-248	222	16	210-232	220	6	204-228	220	9
Interorbital width	216-275	242	13	231-245	238	7	212-245	231	9

Ocean, including the Gulf of Mexico and the Mediterranean and Black seas (Figure 70). Its usual northern limit in the western North Atlantic is Cape Ann, Mass. (Bigelow and Schroeder 1953), but there are records north to Casco Bay, Maine (Nichols and Breder 1927) and to several localities along the outer coast of Nova Scotia (from north to south): Cape Breton Island (McKenzie 1939); Halifax (Jones 1879); Lunenberg (McKenzie 1939); Shag Harbour (Mather and Gibbs 1957); and Pubnico (Vladykov 1935). It is common along the east coast of the United States but becomes uncommon around Miami (D. P. de Sylva, pers. commun.) and the Florida Keys (Schroeder 1924). Although Rivas (1951) stated that there were no records of *S. sarda* from the Gulf of Mexico or Caribbean Sea, there are now several such reports; northern Gulf of Mexico (Boschung 1966) off Pensacola, Fla. (USNM 30692; CAS IU 7825), Dauphin Island, Ala. and the Mississippi Delta (USNM 188420; UMML 7745); Texas (Baughman 1941; Pew, 1954; Hildebrand 1955; USNM 118644-6; CAS SU 18003); the middle of the Gulf (Klawe and Shimada 1959); and Campeche, Mexico (Hildebrand 1955; Springer and Bullis 1956). We have also examined a specimen that was collected by Poey and labelled "Cuba" (MCZ 17047). *Sarda sarda* is apparently absent from most of the Caribbean Sea but is recorded from Colombia (Dahl 1971) and Venezuela (Röhl 1942; Mago Leccia 1970), and we have examined a series of specimens from the Gulf of Cariaco, Venezuela, collected by the RV *Geronimo* in 1966. Fowler (1915) stated that several were seen in the fish market of Port-of-Spain, Trinidad but none were preserved. Published records and museum specimens become more common south of the Amazon: Rio de Janeiro (BMNH 1903.6.9.77, 1923.7.30.303); Santos (Mirando Ribeiro 1918); Rio Grande do Sul (Ihering 1897; MCZ 4739); Argentina from lat. 35° to 38°S (Pozzi and Bordale 1935);

Buenos Aires (Fowler 1926); and Mar del Plata, Argentina (Berg 1895; MACN 5151; MSNG 27472).

Sarda sarda extends further north and south in the eastern than in the western Atlantic, from near Oslo, Norway to Port Elizabeth, South Africa. In Scandinavia it has been taken in Oslo Fjord (Collett 1879a; five ZMO specimens, 425-600 mm FL) and along the Swedish and Danish coasts of the Kattegat (Smitt 1892; Jensen 1937; Lovén 1938; Jensen 1941; Otterstrøm 1943). There is one record from the Netherlands (Hubrecht 1879; Redeke 1941) and there are records from Scotland (Montrose on the east coast, Rae and Pirie 1968; Wigtown on the west coast, Rae and Pirie 1969) and from many counties in Ireland (Farran 1923; Went 1968, 1969, 1971; Wheeler and Blacker 1969, 1972). It is common throughout most of the Mediterranean (Belloc 1954) including the Adriatic Sea (Brünnich 1768; Ninni 1882; Šoljan 1963), Aegean Sea, Sea of Marmora, and the Black Sea (Pallas 1811; Athanassopoulos 1934; Nümann 1955; Demir 1963, 1964; Bănărescu 1964; Svetovidov 1964; MNHN A.6870; USNM 199648; BMNH 1864.4.25.13, 1888.2.3.53). There are records from the four major groups of islands off Europe and Africa: the Azores (Hilgendorf 1888; Collins 1954; USNM skeletons), Madeira (Lowe 1850; BMNH uncat.), Canaries (Valenciennes 1844; Steindachner 1865, 1868; Vinciguerra 1893), and Cape Verdes (Cuvier and Valenciennes 1831; Duméril 1858; Cadenat 1950; Postel 1950). Along the coast of North Africa, there are records from Spanish Morocco (Lozano Cabo 1970), Morocco (Dollfus 1955); Spanish West Africa (Mather and Day 1954); Port Étienne and d'Arguin Bank, Mauritania (Chabanaud and Monod 1927; De Groot and Nijssen 1971); Cape Verde, Sénégal (Rochebrune 1882; Pellegrin 1908; Cadenat 1937; Frade and Postel 1955). *Sarda sarda* is also present in the Gulf of Guinea from Sénégal to Ghana (Irvine 1947; BMNH 1939.7.12.31; Jensen 1967; 23 USNM specimens from the Guinean Trawling Survey; Williams 1968); along the coasts of Angola (Osorio 1890) and South-West Africa (Molteno 1948) through the "Cape Seas" (Barnard 1927) to the Cape of Good Hope (Smith 1949), Mosselbaai (Molteno 1948), and Port Elizabeth, South Africa (SAM uncat.), in the southwestern corner of the Indian Ocean.

Geographic Variation.—For purposes of comparison, *Sarda sarda* was divided into five populations: North America, South America (no vertebral counts available), northeast Atlantic (Scandinavia, Atlantic Europe, and the Azores), Mediterranean Sea (including the Black and Adriatic seas), and Gulf of Guinea (extending south to South Africa). Comparison of meristic characters shows that the two western Atlantic populations are similar to each other as are the Mediterranean and Gulf of Guinea populations. There are differences in a number of characters between combined eastern and combined western Atlantic populations, mostly correlated with higher vertebral counts in the eastern Atlantic. The small northeast Atlantic sample is similar to the other two eastern Atlantic populations but resembles the western Atlantic populations in some characters.

The North American population has 50-53 vertebrae, mode 51, $\bar{x}$ 51.1, compared to a range of 52-55, mode 53, $\bar{x}$ 53.3, for the Mediterranean-Gulf of Guinea (Table 9). Three specimens from the Azores have 51 vertebrae, thus resembling the western Atlantic population. Correlated with vertebral counts, there are fewer fin rays in the western Atlantic (Tables 10-12): dorsal spines modally 21 vs. 22; second dorsal rays modally 16 vs. 17; total second dorsal elements 24 vs. 25; anal rays modally 15 vs. 15 or 16; total anal elements modally 22 skewed toward 21 vs. 22 or 23 skewed toward 22. Independently, there are also fewer gill rakers (Table 7) in the western Atlantic (North America modally 17, $\bar{x}$ 17.6, South America modally 18, $\bar{x}$ 18.7) compared to the eastern Atlantic (Mediterranean and Gulf of Guinea, $\bar{x}$ 20.9)

Based on admittedly small samples, there seems to be a difference between western and eastern Atlantic specimens of *S. sarda* in the size of the caecal mass. Western Atlantic specimens have the caecal mass extending posteriorly for more than half the length of the body cavity in ventral view; eastern Atlantic specimens less than half this distance.

Study material was adequate to compare three areas morphometrically: western Atlantic, Mediterranean Sea, and Gulf of Guinea. There appear to be differences in three characters (Table 21). The western Atlantic population has a lower second dorsal fin (68-90 thousandths of fork length, $\bar{x}$ 80) and a smaller caudal spread (204-235, $\bar{x}$ 222) than do the two eastern Atlantic populations (85-117, $\bar{x}$ 95 and 81-99, $\bar{x}$ 91 for the second dorsal height of the Mediterranean and Gulf of Guinea populations, respectively; 226-270, $\bar{x}$ 247 and 223-289, $\bar{x}$ 253 for the caudal spread). In the snout-

pelvic fin origin distance, the western Atlantic and Mediterranean populations have a longer distance (286-304, $\bar{x}$ 296 and 280-302, $\bar{x}$ 288 respectively) than does the Gulf of Guinea population (267-284, $\bar{x}$ 275).

Of the three widespread species of *Sarda*, there is at least as much justification for recognition of subspecies in *S. sarda* as in *S. chiliensis*. However, there appears to be no available name for the western Atlantic population, the Azores specimens appear intermediate in some characters, and the differences are not great enough to warrant recognition of this population as a distinct subspecies at this time. Additional study is needed on this problem.

Gymnosarda Gill

Gymnosarda Gill 1862:125 (type-species *Thynnus unicolor* Rüppell 1838 by original designation).

Comparative Diagnosis.–The monotypic genus *Gymnosarda* differs from other bonitos in having a well-developed swim bladder, in lacking any intermuscular bones on the back of the skull, and in having more olfactory lamellae (48-56 vs. 21-39 in the other Sardini). It is the only bonito with 19 precaudal and 19 caudal vertebrae. *Gymnosarda* has a differently shaped head than do other bonitos (Tables 1, 22); the interorbital distance is much wider, the eyes are larger, the postorbital distance is shorter, and the distance between the origins of the pectoral and pelvic fins is much larger. The opercular bones are more elongate in *Gymnosarda* than in other bonitos.

Gymnosarda and *Sarda* share characters that distinguish them from *Orcynopsis* and *Cybiosarda*: the bony caudal peduncle keels are well developed, but each keel is divided into anterior and posterior portions on each vertebrae; the spleen is large and prominent in ventral view versus small and not visible in ventral view; the right and left lobes of the liver are both much longer than the middle lobe versus only the right lobe being greatly elongate.

The two genera also differ in several characters. *Gymnosarda* has a pair of glossohyal tooth plates which are absent in *Sarda*. *Gymnosarda* has a naked body; *Sarda* is covered with tiny scales behind the anterior corselet. *Gymnosarda* lacks the horizontal stripes characteristic of *Sarda*. The intestine makes a loop before reaching the anus in *Gymnosarda*; the intestine runs straight from the stomach to the anus in *Sarda*. In ventral view, the spleen is visible on the right side in *Gymnosarda*; it is centrally located in the posterior half of the body cavity in *Sarda*.

TABLE 22.–Morphometric characters of Pacific *Gymnosarda unicolor*. First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

Character	Range	$\bar{x}$	*N*	Kapingamarangi specimens	
Fork length (mm)	240-1040	597	18	875	930
Fork length					
Snout — A	612-651	632	18	650	651
Snout — 2D	545-580	560	18	554	554
Snout — 1D	267-303	292	18	292	303
Snout — P_2	276-306	292	18	298	278
Snout — P_1	251-283	270	18	276	278
P_1 — P_2	123-154	139	16	151	154
Head length	251-275	267	18	297	271
Max. body depth	200-254	222	15	~231	~217
Max. body width	139-176	153	14	—	—
P_1 length	127-188	163	18	180	182
P_2 length	97-120	107	18	120	120
P_2 insertion - vent	321-358	320	16	348	349
P_2 tip - vent	219-251	233	17	—	—
Base 1D	234-284	265	18	258	234
Height 2D	76-121	105	15	120	121
Base 2D	64-102	77	18	73	75
Height anal	76-128	102	17	128	120
Base anal	56- 68	63	18	59	62
Caudal spread	272-344	318	12	328	344
Snout (fleshy)	104-118	109	18	108	108
Snout (bony)	96-106	100	18	98	97
Maxilla length	133-151	140	18	139	136
Post orbital	92-110	101	17	103	103
Orbit (fleshy)	41- 64	53	18	57	57
Orbit (bony)	63- 88	75	16	82	84
Interorbital width	88-110	96	18	104	110
Head length					
Snout (fleshy)	385-430	409	18	403	393
Snout (bony)	355-397	374	18	368	355
Maxilla length	496-550	526	18	524	496
Post orbital	360-409	380	17	388	375
Orbit (fleshy)	161-231	197	18	212	209
Orbit (bony)	232-320	281	16	307	307
Interorbital width	321-400	359	18	391	400

Remarks.–There has been a question as to the valid name for the species in this monotypic genus–*unicolor* Rüppell or *nuda* Günther. The problem arose when Günther placed both *Scomber unicolor* Geoffroy St. Hilaire 1817 and *Thynnus* (*Pelamis*) *unicolor* Rüppell 1838 in the genus *Pelamys* Cuvier 1831. This action made *P. unicolor* Rüppell a junior secondary homonym of *P. unicolor* Geoffroy St. Hilaire so Günther replaced the former name with *P. nuda* Günther. Gill (1862) eliminated the homonomy by describing new genera for both *unicolor* Geoffroy St. Hilaire (*Orcynopsis*) and *unicolor* Rüppell (*Gymnosarda*). We recognize *unicolor* Rüppell as the valid name for the type-species of *Gymnosarda*. Review of the following synonymy shows equal usage of the

names *unicolor* (22 references) and *nuda* (23 references) so there is no reason to favor either name on the grounds of stability.

Gymnosarda unicolor (Rüppell)
Dogtooth Tuna

Thynnus (*Pelamis*) *unicolor* Rüppell 1838:40-41 (original description; Jiddah, Red Sea; pl. 12, fig. 1).

Pelamys nuda Günther 1860:368 (replacement name for *Thynnus unicolor* Rüppell 1838 preoccupied in *Pelamys* by *Scomber unicolor* Geoffroy St. Hilaire 1817). Klunzinger 1871:443-444 (description; Koseir, Red Sea).

Gymnosarda unicolor. Gill 1862:125 (original description of *Gymnosarda*). Chabanaud 1925:198-200 (comparison with *Sarda* and *Orcynopsis*). Fraser-Brunner 1950:149-150 (description), fig. 16. Smith 1956:721 (Aldabra Island), 722 (photograph). Blanc and Postel 1958:370-371 (description, Réunion Island), fig. 1 (viscera), fig. 2 (excised liver). Jones and Silas 1961:380-381 (Port Blair, Andaman Islands; Minicoy Island, Laccadive Archipelago), fig. 7 (after Fraser-Brunner). Jones et al. 1960:136 (Port Blair, Andaman Islands). Postel et al. 1960:392-393 (description; Réunion Island). Collette and Gibbs 1963a:26 (relationships). Collette and Gibbs 1963b:29 (compiled). Gorbunova 1963:87-89, fig. 13, table 11 (19 larvae 8.0-14.0 mm, Indian Ocean). Silas 1963:877-899 (synonymy, description, range, anatomy, biology). Smith and Smith 1963:41 (Seychelles), pl. 31H. Baissac 1964:185-186 (Mascarene waters). Williams 1964:122-124 (Mafia Island, Tanganyika). Talbot 1965:469 (Tutia Reef, Tanganyika). Merrett and Thorp 1966:375 (St. Lazarus Bank, East Africa). Jonklaas 1967:1134 (Maldive Islands), pl. 1 (underwater photo). Jones 1969:26 (Laccadive Archipelago). Nagabhushanam and Chandrasekhara Rao 1972:299, 317, 321 (Laccadive Archipelago). Fukusho and Fujita 1972:32-33 (description, 27 juveniles; Tsushima Island, Korea Straits), fig. 1 (42.9 cm FL juvenile).

Gymnosarda nuda. Kishinouye 1923:426-428 (anatomy; Ryukyu and Ogasawara [Bonin] Islands). Chabanaud 1925:198-199 (comparison with *Sarda* and *Orcynopsis*). Jordan and Hubbs 1925:215 (description; Tokyo market). Fowler 1938:139-140 (description; Tahiti [ANSP 93818]). Marshall 1941:61-62 (first Australian record, Townsville, Queensland). Herre 1945:148 (several records from Philippine Islands). Coates 1950:22 (Barrier Reef), fig. Serventy 1950:19 (Cartier Island and Woodbine Bank, Timor Sea). Warfel 1950:11, 14 (description, Philippine Islands), 15 (fig. 9, lateral view of fish, gill arch, excised liver), 16 (fig. 10, distribution map). La Monte 1952:40 (description), pl. 12. Dung and Royce 1953:tables 93-96 (morphometric data for specimens from Japan, Marshall Islands, Caroline Islands, and Philippine Islands). Herre 1953:248-249 (Philippine records). Fourmanoir 1957:224 (Madagascar, Mauritius, and Comoro Islands), pl. 14, fig. B. Munro 1958b:264 (new records for the New Guinea region: Louisiade Archipelago, Solomon Islands, Woodlark Island, Laughlan Island, Carteret Island, New Ireland, New Britain, Admiralty Islands). Schultz 1960:416-417 (description; Marshall Islands [USNM 140980]). Ronquillo 1963:1723, 1725, 1738, 1739 (length-weight; Philippine Islands), 1732-1733 (gonad index). Marshall 1964:355-356 (description, N. Queensland, Australia), col. pl. 51, fig. 342. Marshall 1966:204, col. pl. 51, fig. 342. Munro 1967:203 (description; New Guinea), pl. 17 (fig. 344). Kami et al. 1968:123 (Guam). Lewis 1968:56 (copepod *Caligus pseudokalumai* described from Eniwetok specimen). Fourmanoir and Griessinger 1971:484 (Rangiroa, Tuamotus). Grant 1972:112 (description; Barrier Reef), col. pl. 17. Bablet 1972:62, 87 (Tuamotu Archipelago).

Misidentification.—*Sarda orientalis*. Smith and Pope 1907:464-465 (77-mm specimen from Urado, Japan [USNM 59638]).

Types.—*Thynnus* (*Pelamis*) *unicolor* Rüppell 1838:40-41, pl. 12, fig. 1. Holotype: SMF 2739; 473 mm FL stuffed specimen; Red Sea, Jiddah; 1834; E. Rüppell. Counts: dorsal fin rays XIII + 13 + VI, but there is probably one more spine concealed in the groove to make the count XIV + 13 + VI; anal fin rays 12 + VI; pectoral fin rays 26; gill rakers cannot be counted (if still present); upper jaw teeth 18; lower jaw teeth (left-right) 14-12.

Distribution.–*Gymnosarda unicolor* is a coral reef species of the tropical Indo-West Pacific (Figure 69). It was originally described by Rüppell (1838) from Jiddah in the Red Sea and was reported by Klunzinger (1871) from Koseir, also in the Red Sea. Western Indian Ocean records include: Tanzania (Mafia Island, Williams 1964; Tutia Reef, Talbot 1965; St. Lazarus Bank, Merrett and Thorp 1966); the Seychelles Islands (Smith and Smith 1963); Amirante Islands (USNM uncat.); Aldabra Island (Smith 1956); Madagascar, Mauritius, and the Comoro Islands (NMC 73-244; Fourmanoir 1957); Réunion Island (Blanc and Postel 1958; Postel et al. 1960) and Mascarene waters (Réunion, Mauritius, and Rodrigues; Baissac 1964). There are records from the Laccadive Archipelago (Jones and Silas 1961; Jones 1969; Nagabhushanam and Chandrasekhara Rao 1972), the Maldive Islands (Jonklaas 1967), Sri Lanka (Ceylon) (Sivasubramaniam 1970), and the Andaman Islands (Jones and Silas 1961; Jones et al. 1960). The only records from the Indonesian area appear to be from Cartier Island and Woodbine Reef in the Timor Sea (Serventy 1950). *Gymnosarda unicolor* is known from several localities in the Philippine Islands (Herre 1945, 1953; Warfel 1950; Dung and Royce 1953; Ronquillo 1963); the New Guinea region–Louisiade Archipelago, Solomon Islands, Woodlark Island, Laughlan Island, Carteret Island, New Ireland, New Britain, and the Admiralty Islands (Munro 1958b); and the northern part of Australia's Great Barrier Reef (Townsville, Marshall 1941; Coates 1950; Marshall 1964). (The record from off Scotland Island, New South Wales (Whitley 1964a) is based on a specimen (AMS IB. 4291) of *Scomberomorus*.) The northern limit of the range is the Sagami Sea (CAS SU 24080, 97 mm FL) and Urado, near Kochi, Shikoku, Japan (USNM 59638, 72 mm FL), the Ryukyu and Bonin islands south of Japan (Kishinouye 1923), and the Straits of Korea (Fukusho and Fujita 1972). To the southeast, there are records or specimens from Guam in the Mariana Islands (Kami et al. 1968), the Palau Islands (CAS GVF), the Carolines (Kapingamarangi and Ifalik, CAS GVF; Pikelot Island in the Truk Islands group, 5 uncataloged USNM specimens; Dung and Royce 1953; Marshalls (Dung and Royce 1953; Schultz 1960; USNM 140980); Gilberts (AMS IB. 5660); Society Islands (Tahiti–Fowler 1938; ANSP 93818); Marquesas Islands (SIO 59-282-43a); Rangiroa Atoll, Tuamotu Archipelago (Fourmanoir and Griessinger 1971; Bablet 1972); and Oeno Island in the Pitcairn Group (BPBM 16966).

Remarks.–Two large specimens from Kapingamarangi Atoll (CAS GVF, 930 and 875 mm FL) require special mention. They have a higher number of very small teeth on the upper (left side, right side 31-29+, 31-30) and lower jaws 22-22, 25-22) than other *Gymnosarda* (Tables 5, 6). Morphometrically, these two Kapingamarangi specimens have distinctly greater snout-anal origin, pectoral to pelvic origin, pelvic fin length, height of second dorsal, height of anal fin, and greater interorbital widths than 18 *Gymnosarda* (240-1,040 mm FL) from throughout the range. The specimens are not very well preserved, but we feel confident that the morphometric differences are real. The differences are not great enough to require the description of a new species, but we cannot fully account for the differences that exist. Additional material, over a wider size range, from Kapingamarangi will be necessary to solve this problem.

Allothunnus Serventy

Allothunnus Serventy 1948:132 (type-species: *Allothunnus fallai* Serventy 1948, by monotypy).

Comparative Diagnosis.–The monotypic genus *Allothunnus* differs from all other scombrids in its very high number of gill rakers. It is the most elongate species of bonito and so has the greatest distances between the snout and the origins of the dorsal and anal fins (Tables 1, 23). The snout and maxilla are shorter than in any other bonito.

Allothunnus differs from all other scombrid genera in having the prootics remarkably extended laterally as wings that frame the posterior margin of the orbit. A pair of dorsolateral processes extend from the parasphenoid up to the prootic wing. *Allothunnus* resembles the Thunnini and differs from all other bonitos in having a prootic pit. Only *Gymnosarda* has a trace of the prominent ridges present on the frontals of *Allothunnus*. The pineal foramen is large and oval in *Allothunnus*, elongate and slit-shaped in all other Sardini and Thunnini. The otoliths are more similar to those of *Sarda* than to those of other bonitos.

The liver has three subequal lobes like *Thunnus*; other bonitos have the right lobe or both right and

left lobes longer than the middle lobe. The nasal rosettes are also more similar to those of *Thunnus* than to those of other bonitos.

Allothunnus fallai Serventy

Allothunnus fallai Serventy 1948:132-135 (original description; Timaru, South Island, New Zealand), fig. 1 (photograph of holotype), fig. 2 (internal gill rakers), fig. 3 (ventral view of liver). Fraser-Brunner 1950:148 (description), fig. 13. Parrott 1958:30-31 (after Serventy). Moreland 1959:30 (New Zealand endemic). Talbot 1960:258-259 (description; Cape Peninsula, South Africa). Olsen 1962:95-96 (description; 4 specimens from southern Tasmania). Collette and Gibbs 1963a:26 (relationships). Collette and Gibbs 1963b:31 (compiled), pl. 9 (after Fraser-Brunner). Jones and Silas 1963:1795 (compiled). Jones and Silas 1964:43-44 (compiled), fig. 8 (after Serventy). Talbot 1964:191-192 (description; anatomy; relationships), pl. 1, fig. 1. Fitch and Craig 1964:199-201 (description; relationships based on otoliths; figs. 3, 5A; California). Whitley 1964a:227 (compiled). Whitley 1964b:48 (listed; Australia). Smith 1965:23 (description; 4 specimens off Walvis Bay, South West Africa), pl. 3, figs. A-B. Nakamura and Kikawa 1966:59-62 (comparison of vertebrae with other scombrids). Nakamura and Mori 1966:67-83 (anatomy, relationships, figs. 1-14; Tasman Sea). Watanabe et al. 1966:85-94 (description of larvae; 100 specimens, 3.2-10.5 mm TL; Indian and South Pacific oceans), figs. 1-5 (larvae 4.0-10.5 mm TL), fig. 6 (distribution map). Tominaga 1966:44-46 (description; specimens from Uruguay and Tasmania), fig. 1B (photo of 870-mm Tasmanian specimen), fig. 2B (first gill arch). Mori 1967a:105-111 (description of 36 larvae from South Atlantic Ocean), figs. 1, 2 (larvae 5.5-13.3 mm TL). Mori 1967b:113-120 (description of 40 juveniles, 96-290 mm FL from stomachs of tunas and marlins from South Pacific), fig. 1 (distribution map). Zharov 1967:220 (*Allothunnus* included in Sardidae). Fierstine and Walters 1968:12 (aspect ratio of caudal fin). Whitley 1968:72 (listed; New Zealand). Ueyanagi 1969:193 (fig. 16e, relationship between occurrence of larvae and ocean structure near New Caledonia). Magnuson 1973:350 (maximum size, no swim bladder, short pectoral fins). Mori 1972:29-31 (juveniles from istiophorid stomach contents; SE of Palau Islands and off South-West Africa), fig. 1 (219-mm juvenile). Warashina and Hisada 1972:51-75 (adults found south of lat. 38°S in the Atlantic, Indian, and Pacific oceans; larvae between lat. 20° and 30°S; juveniles between lat. 25° and 35°S; length-frequency data on 652 specimens 650-960 mm FL). Webb and Wolfe 1974:5-7 (230 tons taken with purse seines off eastern Tasmania, June 1974; fig.).

TABLE 23.—Morphometric characters of *Allothunnus fallai*. First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

Character	Range	$\bar{x}$	N
Fork length (mm)	642-787	734	6
Fork length			
Snout — A	654-688	676	6
Snout — 2D	607-654	628	6
Snout — 1D	291-315	306	6
Snout — P_2	274-294	284	6
Snout — P_1	257-285	269	6
P_1 — P_2	102-116	110	4
Head length	248-272	258	6
Max. body depth	199-239	223	6
Max. body width	159-172	164	4
P_1 length	119-142	129	6
P_2 length	69- 83	78	6
P_2 insertion - vent	356-382	371	6
P_2 tip - vent	276-306	293	6
Base 1D	305-341	319	6
Height 2D	88- 97	93	6
Base 2D	59- 88	72	6
Height anal	82- 98	90	6
Base anal	66- 77	72	6
Caudal spread	210-246	226	3
Snout (fleshy)	70- 79	75	6
Snout (bony)	60- 69	65	6
Maxilla length	91- 96	93	6
Post orbital	136-144	139	4
Orbit (fleshy)	40- 67	45	6
Orbit (bony)	61- 65	63	6
Interorbital width	29- 66	57	6
Head length			
Snout (fleshy)	283-301	292	6
Snout (bony)	242-263	252	6
Maxilla length	354-379	361	6
Post orbital	540-554	545	4
Orbit (fleshy)	153-246	175	6
Orbit (bony)	232-252	244	6
Interorbital width	108-255	224	6

Types.—*Allothunnus fallai* Serventy 1948:132-135. Holotype: Canterbury Museum; 616 mm FL female; New Zealand, South Island, Timaru; 17 July 1916. Two other specimens from the Canterbury Museum are mentioned in the original description and so may be considered paratypes: a cast of a specimen from Kaiapoi, north of Christchurch, dated 4 October 1911 and measuring 920 mm TL and a specimen, 840 mm FL, from Akaroa, Banks Peninsula, dated 4

February 1938. We have not examined any of these and report the counts of the holotype from Serventy's original description: dorsal fin rays XVII+12+VII; anal fin rays 14+VII; pectoral fin rays 25; gill rakers (left-right) 25+48=73, 24+51=75.

Distribution.—*Allothunnus fallai* is found around the world in the Southern Ocean (Figure 69). It was originally described from the South Island of New Zealand in 1948, then reported from Cape Peninsula, South Africa, by Talbot (1960), South-West Africa by Smith (1965), and from Tasmania by Olsen (1962). Fitch and Craig (1964) reported the most unusual record, a 680-mm FL specimen from the Los Angeles-Long Beach harbor complex, the only adult specimen that had been taken north of lat. 35°S. Subsequent to this, Nakamura and Mori (1966) studied several specimens from the Tasman Sea and a series of Japanese authors (Watanabe et al. 1966; Mori 1967a, b; Ueyanagi 1969; Mori 1972) reported juveniles from the southern parts of the Atlantic, Indian, and Pacific oceans to complete our present knowledge of the range of the species. Another scombrid, *Gasterochisma melampus*, and probably also *Thunnus maccoyii*, has a similar distribution in the northern part of the South Ocean around the world.

Food.—One of the Tasmanian specimens reported on by Webb and Wolfe (1974) had its stomach filled with euphausiids. Edward Brinton (SIO) has kindly identified these as *Nyctiphanes australis*, a species endemic to eastern Australian and New Zealand neritic and slope waters.

LITERATURE CITED

ADAMICKA, P.
1972. Funktionsanatomische Untersuchungen am Kopf von Akanthopterygiern (Pisces, Teleostei): *Sarda sarda*, *Pterois volitans*, *Chrysophrys aurata*. Teil I: Einleitung und *Sarda sarda*. [Engl. abstr.] Zool. Jahrb. Anat. 89:301-331.

ALDROVANDI, U.
1613. De piscibus libri v. et de cetis lib. unus. Bononiae, 732 p.

ALLIS, E. P., JR.
1903. The skull, and the cranial and first spinal muscles and nerves in *Scomber scomber*. J. Morphol. 18:45-328.

ANCIETA CALDERON, F.
1963. La pesquería del bonito en el Perú. [Engl. and Fr. abstr.] FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:1607-1619.

1964. Sinopsis sobre la biología y pesquería del "bonito" *Sarda chilensis* (Cuvier y Valenciennes) frente a la costa del Perú. Rev. Fac. Cienc. Biol., Univ. Nac. Trujillo 1(1):17-49.

ATHANASSOPOULOS, G.
1934. Sur la présence des pelamydes (*Pelamys sarda* Bl.) dans la Méditerranée orientale. Comm. Int. Explor. Sci. Mer Médit., Rapp. P.-V. Reun., New Ser., 8:315-316.

BABLET, J. P.
1972. Faune ichtyologique des atolls. *In* Le monde vivant des atolls Polynésie française, Tuamotu-Gambier. Publ. Soc. Océan. 28:57-94.

BAISSAC, J. DE B.
1964. The scombroid fishes of Mascarene waters. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:185-186.

BĂNĂRESCU, P.
1964. Pisces-Osteichthyes (peşti ganoizi şi osoşi). Fauna Repub. Pop. Rom., Vol. 13, 959 p.

BARNARD, K. H.
1927. A monograph of the marine fishes of South Africa. Part II. Ann. S. Afr. Mus. 21:419-1065.

BAUCHOT, M. L., AND M. BLANC.
1961. Catalogue des types de Scombroidei (poissons téléostéens Perciformes) des collections du Muséum National d'Histoire Naturelle de Paris. Bull. Mus. Nat. Hist. Nat. Paris, Ser. 2, 33:369-379.

BAUGHMAN, J. L.
1941. Scombriformes, new, rare, or little known in Texas waters with notes on their natural history or distribution. Trans. Tex. Acad. Sci. 24:14-26.

BÁUZA RULLÁN, J.
1961. Contribuciones al conocimiento de los otolitos de peces actuales. Bol. Real Soc. Esp. Hist. Nat. (B) 59:153-168.

BELLOC, G.
1954. Les thons de la Méditerranée. Première note: germon, pélamide et melva. Proc. Tech. Pap. Gen. Fish. Counc. Medit., FAO (Food Agric. Organ. U.N.) 2:283-318.

BELON, P.
1553. De aquatilibus, libri duo cum eiconibus ad vivam ipsorum effigiem, quoad eius fieri potuit, expressis. Paris, 448 p.

BEN-TUVIA, A.
1971. Revised list of the Mediterranean fishes of Israel. Isr. J. Zool. 20:1-39.

BERG, C.
1895. Enumeración sistemática y sinonímica de los peces de las costas Argentina y Uruguaya. An. Mus. Nac. Buenos Aires 4:1-120.

BERRY, F. H.
1969. *Elegatis bipinnulata* (Pisces: Carangidae): Morphology of the fins and other characters. Copeia 1969:454-463.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53:1-577.

BINI, G.
1968. Atlante dei pesci delle coste Italiane, Vol. VI. Osteitti. Mondo Sommerso Editrice, Milan, 177 p.

BLACHE, J., J. CADENAT, AND A. STAUCH.
1970. Clés de détermination des poissons de mer signalés dans l'atlantique oriental entre le 20e parallèle Nord et le 15e parallèle Sud. Faune Tropicale XVIII, O.R.S.T.O.M., Paris, 480 p.

BLANC, M., AND M. L. BAUCHOT.
1964. Les Scombroidei (poissons téléostéens Perciformes) du Muséum National d'Histoire Naturelle de Paris. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:443-458.

BLANC, M., AND E. POSTEL.
1958. Sur une petite collection de poissons de la Réunion. Mém. Inst. Sci. Madagascar, Ser. F, Oceanogr. 2:367-376.

BLOCH, M. E.
1793. Naturgeschichte der äuslandischen Fische. Königl. Akad. Kunst. J. Morino Comp., Berlin, Part 7, 144 p.

BLOCH, M. E., AND J. G. SCHNEIDER.
1801. Systema Ichthyologiae. Berlin, 584 p.

BOESEMAN, M.
1947. Revision of the fishes collected by Burger and Von Siebold in Japan. Zool. Meded Rijksmus. Nat. Hist. Leiden 28:1-242.
1964. Scombroid types in the Leiden Museum collection. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:461-468.

BONAPARTE, C. L.
1831. Saggio d'una distribuzione metodica degli animali vertebrati a sangue freddo. Gior. Arcad. Sci. Lett. Art., Rome 53:129-209.
1845. Catalogo metodico dei pesci Europei. Atti Sci. Ital. 1845:1-95.

BOSCHUNG, H. T., JR.
1966. The occurrence of the common bonito, *Sarda sarda*, in the northern Gulf of Mexico. Trans. Am. Fish. Soc. 95:227-228.

BROCK, V. E.
1949. A preliminary report on *Parathunnus sibi* in Hawaiian waters and a key to the tunas and tuna-like fishes of Hawaii. Pac. Sci. 3:271-277.

BRÜNNICH, M. T.
1768. Ichthyologia Massiliensis, sistens piscium descriptiones eorumque apud incolas nomina. Accedunt Spolia Maris Adriatici. Hafnea et Lipsiae, 110 p.

BURNE, R. H.
1909. The anatomy of the olfactory organ of teleostean fishes. Proc. Zool. Soc. Lond. 1909:610-663.

BUEN, F. DE.
1930a. Ictiología española. I. Scombriformes y Thunniformes. Bol. Oceanogr. Pesca Madrid 15(162):34-53.
1930b. Estados larvarios y juveniles de la *Sarda sarda* (Bloch). Inst. Español Oceanogr. Trabajos 3:32 p.
1958. Peces del suborden Scombroidei en aguas de Chile. Rev. Biol. Mar., Valparaiso 7:3-38.

BUEN, F. DE, AND F. FRADE.
1932. Clef dichotomique pour une classification rapide (d'après les caractères de coloration et très apparents de la morphologie externe). Comm. Int. Explor. Sci. Mer Medit. Rapp. P.-V., New Ser., 7:71-74.

CADENAT, J.
1937. Recherches systématiques sur les poissons littoraux de la Côte Occidentale d'Afrique, récoltés par le navire *Président Théodore-Tissier*, au cours de sa 5^{e} croisière (1936). Rev. Trav. Off. Sci. Tech. Pêch. Marit. 10:425-562.
1950. Notes sur quelques Scombridae des Îles du Cap-Vert. Congr. Pêches Pêcheries, l'Union Fr. d'Outre-Mer, p. 131-134.

CANESTRINI, G.
1870. Pesci. *In* E. Cornalia (editor), Fauna d'Italia.

CAREY, F. G., J. M. TEAL, J. W. KANWISHER, AND K. D. LAWSON.
1971. Warm-bodied fish. Am. Zool. 11:135-143.

CARUS, J. V.
1893. Prodromus faunae Mediterraneae. Vertebrata. 1. Class. Pisces. E. Schweiz., Stuttg. 2:498-711.

CHABANAUD, P.
1925. Sur quelques Scombroides de la côte occidentale d'Afrique. Bull. Soc. Zool. Fr. 50:197-201.
1944. *Sarda chiliensis* (C.V.). Remarques diverses. Bull. Inst. Océanogr. Monaco 860:1-6.

CHABANAUD, P., AND T. MONOD.
1927. Les poissons de Port-Étienne. Bull. Comit. Etud. Hist. Sci. Afr. Occident. Fr. 1926:225-287.

CHAINE, J.
1957. Recherches sur les otolithes des poissons. Étude descriptive et comparative de la sagitta des téléostéens. Description des espèces. Bull. Cent. Etud. Rech. Sci. Biarritz 1:463-557.

CHEVEY, P.
1934. Révision synonymique de l'oeuvre ichtyologique de G. Tirant. Inst. Océanogr. Indochine, Stn. Mar. Cauda, Note 7, 291 p.

CHIRICHIGNO F., N.
1969. Lista sistematica de los peces marinos comunes para Ecuador, Peru, y Chile. Conf. Explot. Conserv. Riquezas Marit. Pac. Sur, 108 p.

CLEMENS, W. A., AND G. V. WILBY.
1961. Fishes of the Pacific coast of Canada. 2nd ed. Fish. Res. Board Can., Bull. 68, 443 p.

CLOTHIER, C. R.
1950. A key to some southern California fishes based on vertebral characters. Calif. Div. Fish Game, Fish Bull. 79, 83 p.

COATES, G.
1950. Fishing on the Barrier Reef and inshore. T. Willmett and Sons, Townsville, 72 p.

COLLETT, R.
1879a. Meddelelser om Norges Fiske i Aarene 1875-1878. Forh. Vidensk.-Selsk. Christ. 1:1-107.
1879b. Om den saakaldte *Thynnus peregrinus*, Coll., 1879. Forh. Vidensk.-Selsk. Christ. 15, 3 p.

COLLETTE, B. B.
1966. Revue critique des types de Scombridae des collections du Muséum National d'Histoire Naturelle de Paris. [Engl. summ.] Bull. Mus. Natl. Hist. Nat. Paris, Ser. 2, 38:362-375.
1970. *Rastrelliger kanagurta*, another Red Sea immigrant into the Mediterranean Sea, with a key to the Mediterranean species of Scombridae. Bull. Sea Fish. Res. Stn. Haifa 54, p. 3-6.

COLLETTE, B. B., AND R. H. GIBBS, JR.
1963a. A preliminary review of the fishes of the family Scombridae. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:23-32.
1963b. Preliminary field guide to the mackerel- and tuna-like fishes of the Indian Ocean (Scombridae). Smithson. Inst., 48 p.

COLLINS, B. L.
1954. Lista de peixes dos mares dos Açores. Açoreana 5(2):103-142.

CONRAD, G. M.
1938. The osteology and relationships of the wahoo (*Acanthocybium solandri*), a scombrid fish. Am. Mus. Nat. Hist. Novit. 1000, 32 p.

CUVIER, G.
1829. Le règne animal. Nouvelle ed. tom. II. Deterville, Paris, 406 p.

CUVIER, G., AND A. VALENCIENNES.
1831. Histoire naturelle des poissons, Vol. 8. F. G. Levrault, Paris, 375 p.

DAHL, G.
1971. Los peces del norte de Colombia. INDERENA, Bogotá, 391 p.

DAVID, L. R.
1943. Miocene fishes of southern California. Geol. Soc. Am., Spec. Pap. 43, 193 p.

DAY, F.
1878. The fishes of India; being a natural history of the fishes known to inhabit the seas and fresh waters of India, Burma, and Ceylon, 1:1-320. Bernard Quaritch, Lond.

DE GROOT, S. J., AND H. NIJSSEN.
1971. Notes on the fishes collected by the R. V. "Tridens" on the north west African Shelf, 19-25 January 1969. Bijdr. Dierkd. 41:1-9.

DELAROCHE, F. E.
1809. Suite du mémoire sur les espèces de poissons observées a Iviça. Ann. Mus. Hist. Nat. Paris 13:313-361.

DEMIR, M.
1963. Synopsis of biological data on bonito *Sarda sarda* (Bloch) 1793. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:101-129.
1964. Distribution of meristic counts of common bonito (*Sarda sarda* Bl.) from Turkish waters. [Fr. abstr.] Proc. Tech. Pap. Gen. Fish. Counc. Medit., FAO (Food Agric. Organ. U.N.) 7:455-457.

DE SYLVA, D. P.
1955. The osteology and phylogenetic relationships of the blackfin tuna, *Thunnus atlanticus* (Lesson). Bull. Mar. Sci. Gulf Caribb. 5:1-41.

DIEUZEIDE, R.
1930. Sur quelques scombriniens des côtes algériennes. Bull. Trav. Stn. Aquicult. Pêche, Castiglione, Alger [1929], fasc. 2, p. 127-167.

DIEUZEIDE, R., M. NOVELLA, AND J. ROLAND.
1955. Catalogue des poissons des côtes algériennes. III. Ostéoptérygiens. Bull. Stn. Aquicult. Pêche Castiglione, New Ser. 6, 384 p.

DOLLFUS, R. P.
1955. Première contribution a l'établissement d'un fichier ichthyologique de Maroc Atlantique de Tanger a l'embouchure de l'oued Dra. Trav. Inst. Sci. Chérifien, Zool. Sér. 6, 227 p.

DORNESCU, G. T., AND D. MIŞCALENCU.
1969. Cele trei tripuri de branhii ale Teleosteenilor. [Russ. and Fr. summ.] Anal Univ. Bucureşti, Ser. Stiint. Nat. Biol. 17:11-20.

DRESSLAR, F. B., AND B. FESLER.
1889. A review of the mackerels (Scombrinae) of America and Europe. Bull. U.S. Fish Comm. 7:429-446.

DUHAMEL DU MONCEAU, H. L.
1769. Traité général des pêsches, et histoire des poissons qu'elles fournissent. . . . Paris.

DUMÉRIL, A.
1858. Reptiles et poissons d l'Afrique occidentale. Arch. Mus. Hist. Nat. Paris 10:137-268.

DUNG, D. I. Y., AND W. F. ROYCE.
1953. Morphometric measurements of Pacific scombrids. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 95, 170 p.

ECONOMIDIS, P. S.
1972. Catalogue des poissons de la Grèce. [In Greek, Fr. summ.] Hellenic Oceanol. Limnol. 11:421-598.

EHRENBAUM, E.
1924. Scombriformes. Rep. Dan. Oceanogr. Exped. 1908-1910, II (Biology) A, 11, 42 p.

ERDMAN, D. S.
1971. Notes on fishes from the Gulf of Nicoya, Costa Rica. Rev. Biol. Trop. 19(1, 2):59-71.

FARRAN, G. P.
1923. Rare fishes in Irish Waters. Irish Nat. (Dublin) 33(10):106-107.

FIERSTINE, H. L., AND V. WALTERS.
1968. Studies in locomotion and anatomy of scombroid fishes. Mem. South. Calif. Acad. Sci. 6:1-31.

FILIPPI, F. DE, AND G. B. VERANY.
1859. Sopra alcuni pesci nuovi o poco noti del Mediterraneo. Mem. Reale Accad. Sci. Torino, Ser. 2, 18:187-199.

FITCH, J. E., AND W. L. CRAIG.
1964. First records for the bigeye thresher (*Alopias superciliosus*) and slender tuna (*Allothunnus fallai*) from California, with notes on eastern Pacific scombrid otoliths. Calif. Fish Game 50:195-206.

FOOD AND AGRICULTURAL ORGANIZATION OF THE UNITED NATIONS.
1973. Catches and landings, 1972. FAO Yearb. Fish. Stat. 34, 560 p.

FOURMANOIR, P.
1957. Poissons téléostéens des eaux malgaches du Canal de Mozambique. Mém. Inst. Sci. Madagascar, Ser. F, Oceanogr. 1:1-316.

FOURMANOIR, P., AND M. GRIESSINGER.
1971. Poissons de Rangiroa. Cah. O.R.S.T.O.M., Sér. Océanogr. 9:475-489.

FOWLER, H. W.
1915. The fishes of Trinidad, Grenada, and St. Lucia, British West Indies. Proc. Acad. Nat. Sci. Phila. 67:520-546.
1926. Fishes from Florida, Brazil, Bolivia, Argentina, and Chile. Proc. Acad. Nat. Sci. Phila. 78:249-285.
1928. The fishes of Oceania. Mem. Bernice P. Bishop Mus. 10, 540 p.
1936. The marine fishes of West Africa based on the collection of the American Museum Congo expedition, 1909-1915. Part II. Bull. Am. Mus. Nat. Hist. 70:607-1493.
1938. The fishes of the George Vanderbilt South Pacific expedition, 1937. Acad. Nat. Sci. Phila., Monogr. 2, 349 p.
1944. The fishes. *In* Results of the fifth George Vanderbilt Expedition (1941) (Bahamas, Caribbean Sea, Panama, Galápagos Archipelago and Mexican Pacific Islands), p. 57-529. Acad. Nat. Sci. Phila., Monogr. 6.
1949. The fishes of Oceania—Supplement 3. Mem. Bernice P. Bishop Mus. 12(2):37-185.

FRADE, F., AND F. DE BUEN.
1932. Poissons Scombriformes (excepté la famille Scombridae). Clef de classification principalement d'après la morphologie interne. Comm. Int. Explor. Sci. Mer Mèdit. Rapp. P.-V. Reun. 7:69-70.

FRADE, F., AND E. POSTEL.
1955. Contribution à l'etude de la reproduction des scombridés et thonidés de l'Atlantique tropical. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 137:33-35.

FRASER-BRUNNER, A.
1950. The fishes of the family Scombridae. Ann. Mag. Nat. Hist., Ser. 12, 3:131-163.

FUKUSHO, K., AND S. FUJITA.
1972. Notes on the young of dogtooth tuna caught in the waters of Tsushima Island. [In Jap., Engl. abstr.] Jap. J. Ichthyol. 19:32-33. (Natl. Mar. Fish. Serv. Syst. Lab. Transl. 70)

GEOFFROY SAINT-HILAIRE, E.
1817. Poissons de la Mer Rouge et de la Méditerranée. *In* Description de l'Egypte. . . ., Paris, Planches Histoire Naturelle, 1, Poissons, pl. 18-27.

GEOFFROY SAINT-HILAIRE, I.
1827. Histoire naturelle des poissons de la Mer Rouge et de la Méditerranée. Description de l'Egypte. . ., Paris, Histoire Naturelle 1:311-340.

GEORGE, C. J., V. A. ATHANASSIOU, AND I. BOULOS.
1964. The fishes of the coastal waters of Lebanon. Am. Univ. Beirut, Misc. Pap. Nat. Sci. 4, 27 p.

GIBBS, R. H., JR., AND B. B. COLLETTE.
1967. Comparative anatomy and systematics of the tunas, genus *Thunnus*. U.S. Fish. Wildl. Serv., Fish. Bull. 66:65-130.

GIGLIOLI, E. H.
1880. Elenco dei mammiferi, degli uccelli e dei rettili ittifagi appartenenti alla fauna italica e catalogo degli anfibi e dei pesci italiani. Espos. Int. Pesca Berlin, 1880, 55 p.

GILBERT, C. H., AND E. C. STARKS.
1904. The fishes of Panama Bay. Mem. Calif. Acad. Sci. 4, 304 p.

GILL, T. N.
1862. On the limits and arrangement of the family of scombroids. Proc. Acad. Nat. Sci. Phila. 1862:124-127.

GIRARD, C.
1859. Fishes. *In* Reports of explorations and surveys to survey the most practical and economical route for a railroad from the Mississippi River to the Pacific Ocean. Vol. X.

GISTEL, J.
1848. Naturgeschichte des Thierreichs. Für höhere Schulen. Scheitlin and Krais, Stuttgart, 216 p.

GNANAMUTTU, J. C.
1968. On the occurrence of the oriental bonito, *Sarda orientalis* (Temminck and Schlegel) along the Madras coast. J. Mar. Biol. Assoc. India 8:365.
1971. Osteology of the Indian mackerel, *Rastrelliger kanagurta* (Cuvier). Indian J. Fish. 13:1-26.

GODSIL, H. C.
1954. A descriptive study of certain tuna-like fishes. Calif. Dep. Fish Game, Fish Bull. 97, 185 p.
1955. A description of two species of bonito, *Sarda orientalis* and *S. chiliensis* and a consideration of relationships within the genus. Calif. Dep. Fish Game, Fish Bull. 99, 43 p.

GOODING, R. M.
1963. The olfactory organ of the skipjack *Katsuwonus pelamis*. [Fr. and Span. abstr.] FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:1621-1631.

GORBUNOVA, N. N.
1963. Larvae of scombroid fishes (Pisces, Scombriformes) from the Indian Ocean. [In Russ., Engl. summ.] Tr. Inst. Okeanol. Akad. Nauk SSSR 62:68-95.

GORDON, B. L.
1960. The marine fishes of Rhode Island. Book and Tackle Shop, Watch Hill, R.I., 136 p.

GRANIER, J.
1968. Les Scombres dans le Golfe d'Aigues-Mortes. Bull. Mens. Soc. Linn. Lyon 37(8):324-330.

GRANT, E. M.
1972. Guide to fishes. 2nd ed. Queensland Dep. Primary Ind., Brisbane, 472 p.

GRIFFINI, A.
1903. Ittiologia italiana. Ulrico Hoepli, Milan, 469 p.

GRUVEL, A., AND A. BOUYAT.
1906. Les pêcheries de la côte occidentale d'Afrique. A. Challamel, Paris, 280 p.

GUICHENOT, A.
1850. Histoire naturelle des reptiles et des poissons. Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842. Sci. Phys., Zool. Vol. 5 (3), 128 p.

GÜNTHER, A.
1860. Catalogue of the acanthopterygian fishes in the collection of the British Museum. Vol. 2, 548 p.

HART, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can., Bull. 180, 740 p.

HERRE, A. W.
1936. Fishes of the Crane Pacific Expedition. Field Mus. Nat. Hist., Zool. Ser., 21:1-472.
1945. Additions to the fish fauna of the Philippine Islands. Copeia 1945:146-149.
1953. Check list of Philippine fishes. U.S. Fish Wildl. Serv., Res. Rep. 20, 977 p.

HILDEBRAND, H. H.
1955. A study of the fauna of the pink shrimp (*Penaeus duorarum* Burkenroad) grounds in the Gulf of Campeche. Publ. Inst. Mar. Sci., Univ. Tex. 4(1):169-232.

HILDEBRAND, S. F.
1946. A descriptive catalog of the shore fishes of Peru. U.S. Natl. Mus. Bull. 189, 530 p.

HILGENDORF, F. M.
1888. Die Fische der Azoren. Arch. Naturgesch. 54(1):205-213.

HOLMGREN, U.
1958. On the pineal organ of the tuna, *Thynnus thynnus* L. Breviora 100, 5p.

HONMA, Y.
1952. A list of the fishes collected in the Province of Echigo, including Sado Island. [In Jap.] Jap. J. Ichthyol. 2:138-146.

HUBRECHT, A. A. W.
1879. [Mededeeling over de vangst van *Pelamys sarda* C V in Juni 1878 nabij Bergen-op-Zoom] Tweede Jaarversl. Zool. Stn. Tijdschr. Ned. Dierk. Ver. 4:9.

IDYLL, C. P., AND D. P. DE SYLVA.
1963. Synopsis of biological data on bonito *Sarda sarda* (Bloch) 1793 (Western Atlantic). FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:755-760.

IHERING, H. VON.
1897. Os peixes da costa do mar no Estado do Rio Grande do Sul. Rev. Mus. Paulista 2:25-63.

IONESCU, N., N. GADIDOV, AND S. STĂNESCU.
1958. Contribuţii la cunoaşterea biologiei, şi persecuitului pălămidei (*Sarda sarda* Bloch), în apele Romînești ale Mării Negre în perioada 1954-1956. Hidrobiologia 1:165-186.

IRVINE, F. R.
1947. The fishes and fisheries of the Gold Coast. Crown Agents for the Colonies, Lond., 352 p.

IWAI, T., AND I. NAKAMURA.
1964a. Branchial skeleton of the bluefin tuna, with special reference to the gill rays. Bull. Misaki Mar. Biol. Inst., Kyoto Univ. 6:21-25.

1964b. Olfactory organs of tunas with special reference to their systematic significance. Bull. Misaki Mar. Biol. Inst., Kyoto Univ. 7:1-8.

JENSEN, A. J. C.
1937. Seasonal guests in transition area. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 102(6):1-18.

JENSEN, A. S.
1941. Om nogle for den danski fauna nye eller sjaeldne fiskearter. Vidensk. Medd. Dan. Naturhist. Foren. Kbh. 104:179-206.

JENSEN, A. C.
1967. Observations on pelagic fishes off the west coast of Africa. Bull. Mar. Sci. 17:42-51.

JONES, J. M.
1879. List of the fishes of Nova Scotia. Proc. Trans. N. S. Inst. Nat. Sci. 5(1):87-97.

JONES, S.
1961. Notes on eggs, larvae and juveniles of fishes from Indian waters. VI. Genus *Auxis* Cuvier. VII. *Sarda orientalis* (Temminck & Schlegel). Indian J. Fish. 7:337-347.
1969. Catalogue of fishes from the Laccadive Archipelago in the reference collections of the Central Marine Fisheries Research Institute. Bull. Cent. Mar. Fish. Res. Inst. 8, 32 p.

JONES, S., AND M. KUMARAN.
1964. Eggs, larvae and juveniles of Indian scombroid fishes. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:343-378.

JONES, S., AND E. G. SILAS.
1961. Indian tunas-A preliminary review, with a key for their identification. Indian J. Fish. 7:369-393.
1963. Tuna and tuna-like fishes from the Indian seas. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:1775-1796.
1964. A systematic review of the scombroid fishes of India. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:1-105.

JONES, S., E. G. SILAS, AND E. DAWSON.
1960. New records of scombroid fishes from the Andaman-Nicobar waters. J. Mar. Biol. Assoc. India 2:136-137.

JONKLAAS, R.
1967. Scombroid fishes and fisheries of the Maldive Islands with special reference to the tuna fishery. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:1132-1138.

JORDAN, D. S., AND B. W. EVERMANN.
1896. The fishes of North and Middle America. Bull. U.S. Natl. Mus. 47, 1240 p.

JORDAN, D. S., AND C. H. GILBERT.
1882. Synopsis of the fishes of North America. Bull. U.S. Natl. Mus. 16, 1018 p.

JORDAN, D. S., AND C. L. HUBBS.
1925. Record of fishes obtained by David Starr Jordan in Japan, 1922. Mem. Carnegie Mus. 10:93-346.

JORDAN, D. S., AND E. K. JORDAN.
1922. A list of the fishes of Hawaii, with notes and descriptions of new species. Mem. Carnegie Mus. 10:1-92.

JORDAN, D. S., AND J. O. SNYDER.
1900. A list of fishes collected in Japan by Keinosuke Otaki, and by the United States steamer Albatross, with descriptions of fourteen new species. Proc. U.S. Natl. Mus. 23:335-380.
1901. A preliminary check list of the fishes of Japan. Annot. Zool. Jap. 3(2-3):31-159.
1904. Description of a new species of fish (*Apogon evermanni*) from the Hawaiian Islands, with notes on other species. Proc. U.S. Natl. Mus. 28:123-126.

JORDAN, D. S., S. TANAKA, AND J. O. SNYDER.
1913. A catalogue of the fishes of Japan. J. Coll. Sci., Imp. Univ., Tokyo 33(1):1-497.

KAMI, H. T., I. I. IKEHARA, AND F. P. DELEON.
1968. Check-list of Guam fishes. Micronesica 4:95-131.

KIKAWA, S., AND STAFF.
1963. Synopsis of biological data on bonito *Sarda orientalis* Temminck and Schlegel 1842. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:147-156.

KISHINOUYE, K.
1923. Contributions to the comparative study of the so-called scombroid fishes. J. Coll. Agric., Imp. Univ., Tokyo 8:293-475.

KLAWE, W. L.
1961a. Young scombroids from the waters between Cape Hatteras and Bahama Islands. Bull. Mar. Sci. Gulf Caribb. 11:150-157.
1961b. Notes on larvae, juveniles, and spawning of bonito (*Sarda*) from the eastern Pacific Ocean. Pac. Sci. 15:487-493.
1962. Bonito juvenil (*Sarda chiliensis*) en las aguas del sur de Baja California. Ciencia (Mexico) 21:180.

KLAWE, W. L., AND B. M. SHIMADA.
1959. Young scombroid fishes from the Gulf of Mexico. Bull. Mar. Sci. Gulf Caribb. 9:100-115.

KLUNZINGER, C. B.
1871. Synopsis der Fische des Rothen Meeres. II. Verh. Zool.-Bot. Ges. Wien 21:441-668.

KUMARAN, M.
1964. Studies on the food of *Euthynnus affinis affinis* (Cantor), *Auxis thazard* (Lacépède), *Auxis thynnoides* Bleeker and *Sarda orientalis* (Temminck and Schlegel). Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:599-606.

KUO, C.-M.
1970. Taxonomic, growth, and maturation studies on the bonitos of the temperate eastern Pacific Ocean. Ph.D. Thesis, Univ. California, San Diego, 321 p.

LAEVASTU, T., AND H. ROSA, JR.
1963. Distribution and relative abundance of tunas in relation to their environment. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:1835-1851.

LA MONTE, F.
1945. North American game fishes. Doubleday, Doran and Company, Inc., Garden City, N.Y., 202 p.
1952. Marine game fishes of the world. Doubleday & Company, Inc., Garden City, N.Y., 190 p.

LE GALL, J.
1934a. *Orcynopsis unicolor*. Species account 287. Cons. Perm. Int. Explor. Mer, Faune Ichthyol. Atl. Nord., Vol. 15.
1934b. *Sarda sarda*. Species account 288. Cons. Perm. Int. Explor. Mer, Faune Ichthyol. Atl. Nord., Vol. 15.

LEWIS, A. G.
1968.Copepod crustaceans parasitic on fishes of Eniwetok Atoll. Proc. U.S. Natl. Mus. 125:1-78.

LIEBMAN, E.
1934. Contributions to the knowledge of Palestine sea fishes. Comm. Int. Explor. Sci. Mer. Médit., Rapp. P.-V. Réun., New Ser., 8:317-327.

LORD, C. E.
1927. A list of the fishes of Tasmania. J. Pan-Pac. Res. Inst. 2(4):11-16.

LOVÉN, M.
1938. Den ryggstrimmiga pelamiden *Sarda sarda* Bloch och dess förekomst i nordiska farvatten. Fauna Flora 33(6):274-280.

LOWE, R. T.
1850. An account of fishes discovered or observed in Madeira since the year 1842. Proc. Zool. Soc. Lond. 18:247-253.

LOZANO, L.
1916. Sobre el hallazgo de un *Orcynopsis unicolor* (Geoffr.) en Melilla. Bol. R. Soc. Esp. Hist. Nat. 16:298-302.

LOZANO CABO, F.
1970. Caractéristiques zoogéographiques de la faune ichthyologique des côtes de îles Canaries, du Maroc, du Sahara espagnol et de la Mauritanie avec une étude speciale des poissons côtiers. Rapp. P.-V. Réun., Cons. Perm. Int. Explor. Mer 159:152-164.

LOZANO Y REY, L.
1952. Peces fisoclistos, subserie toracicos. Segunde parte. Mem. R. Acad. Cienc. Exactas. Fís. Nat., Madr. Ser. Cienc. Nat. 14:387-703.

MACLEAY, W.
1880. Descriptive catalogue of the fishes of Australia. Part II. Proc. Linn. Soc. N.S.W. 5(4):510-629.

MAGNUSON, J. J.
1973. Comparative study of adaptations for continuous swimming and hydrostatic equilibrium of scombroid and xiphoid fishes. Fish. Bull., U.S. 71:337-356.

MAGNUSON, J. J., AND J. G. HEITZ.
1971. Gill raker apparatus and food selectivity among mackerels, tunas, and dolphins. Fish. Bull., U.S. 69:361-370.

MAGNUSON, J. J., AND J. H. PRESCOTT.
1966. Courtship, locomotion, feeding, and miscellaneous behaviour of Pacific bonito (*Sarda chiliensis*). Anim. Behav. 14:54-67.

MAGO LECCIA, F.
1958. The comparative osteology of the scombroid fishes of the genus *Scomberomorus* from Florida. Bull. Mar. Sci. Gulf Caribb. 8:299-341.
1970. Lista de los peces de Venezuela, incluyendo un estudio preliminar sobre la ichtiogeografía del país. Minist. Agric. Cria, Of. Nac. Pesca, Caracas, 283 p.

MANN F., G.
1954. La vida de los peces en aguas Chilenas. 2nd ed. Ministerio de Agricultura, Santiago de Chile, 339 p.

MANSUETI, R. J.
1962. The Atlantic bonito, *Sarda sarda*, in northern Chesapeake Bay, and comments on the seaside fishery of Maryland. Chesapeake Sci. 3:47-49.

MANZER, J. I.
1965. *Sarda lineolata* (Girard), a Pacific bonito in the Strait of Georgia, British Columbia. J. Fish. Res. Board Can. 22:853-855.

MARR, J. C., AND M. B. SCHAEFER.
1949. Definitions of body dimensions used in describing tunas. U.S. Fish Wildl. Serv., Fish. Bull. 51:241-244.

MARSHALL, T. C.
1941. New ichthyological records. Mem. Queensl. Mus. 12:53-64.
1964. Fishes of the Great Barrier Reef and coastal waters of Queensland. Angus and Robertson, Sydney, 566 p. Also 1965, Livingston Publishing Company, Narbeth, Pa.
1966. Tropical fishes of the Great Barrier Reef. Angus and Robertson, Sydney, 239 p.

MATHER, F. J. III, AND C. G. DAY.
1954. Observations of pelagic fishes of the tropical Atlantic. Copeia 1954:179-188.

MATHER, F. J. III, AND R. H. GIBBS, JR.
1957. Distributional records of fishes from waters off New England and the middle Atlantic states. Copeia 1957:242-244.

MCCOY, F.
1888. Prodromus of the zoology of Victoria. 1(16):203-251. Gov. Printer, Melbourne.

MCCULLOCH, A. R.
1922. Check list of the fish and fish-like animals of New South Wales. Part 3. Aust. Zool. 2:86-130.

MCKENZIE, R. A.
1939. Some marine fish and salp records. Proc. Nova Scotia Inst. Sci. 20:13-20.

MEEK, S. E., AND S. F. HILDEBRAND.
1923. The marine fishes of Panama. Field Mus. Nat. Hist., Publ. 215, Zool. Ser. 15, Part 1, 330 p.

MERRETT, N. R., AND C. H. THORP.
1966. A revised key to the scombroid fishes of East Africa with new observations on their biology. Ann. Mag. Nat. Hist., Ser. 13, 8:367-384.

MIRANDA RIBEIRO, A. DE
1918. Lista dos peixes Brasileiros do Museu Paulista. 3ª Parte. Rev. Mus. Paul. 10:763-783.

MOLTENO, C. J.
1948. The South African tunas - a preliminary study of the economic potentialities. S. Afr. Fish. Ind. Res. Inst., Cape Town, 34 p.

MONOD, T.
1968. Le complexe urophore des poissons téléostéens. Mém. Inst. Fond. Afr. Noire 81, 705 p.

MORÉAU, E.
1881. Histoire naturelle des poissons de la France, vol. 2. G. Masson, Paris, 570 p.

MORELAND, J.
1959. The composition, distribution and origin of the New Zealand fish fauna. Proc. N. Z. Ecol. Soc. 6:28-30.

MORI, K.
1967a. Occurrence of the larvae of *Allothunnus fallai* Serventy in the South Atlantic Ocean. Rep. Nankai Reg. Fish. Res. Lab. 25:105-111.
1967b. Record of occurrence and some notes on young slender-tuna (*Allothunnus fallai* Serventy) from the stomachs of longline tunas and marlins in the South Pacific Ocean. Rep. Nankai Reg. Fish. Res. Lab. 25:113-120.
1972. Records of juveniles of slender tuna, *Allothunnus fallai*, from the equatorial western Pacific and the South Atlantic Ocean. [In Jap., Engl. abstr.] Jap. J. Ichthyol. 19:29-31. [Natl. Mar. Fish. Serv., Syst. Lab. Transl. 70.]

MORICE, J.
1953a. Essai systématique sur les familles des Cybiidae, Thunnidae et Katsuwonidae, poissons Scombroïdes. Rev. Trav. Inst. Sci. Tech. Pêches Marit. 18(1):35-63.
1953b. Un caractère systématique pouvant servir à séparer les espèces de Thunnidae atlantiques. Rev. Trav. Inst. Sci. Tech. Pêches Marit. 18(1):65-74.

MUIR, B. S.
1969. Gill dimensions as a function of fish size. J. Fish. Res. Board Can. 26:165-170.
1970. Contribution to the study of blood pathways in teleost gills. Copeia 1970:19-28.

MUNRO, I. S. R.
1958a. Handbook of Australian fishes, No. 28:113-116. Fish. Newsl. 17(10):17-20.
1958b. The fishes of the New Guinea region. Papua New Guinea Agric. J. 10(4):97-369.
1967. The fishes of New Guinea. Dep. Agric., Stock, Fish., Port Moresby, New Guinea, 650 p.

NAGABHUSHANAM, A. K., AND G. CHANDRASEKHARA RAO.
1972. An ecological survey of the marine fauna of Minicoy Atoll (Laccadive Archipelago, Arabian Sea). Mitt. Zool. Mus. Berl. 48:265-324.

NAIR, R. V., K. VIRABHADRA RAO, AND K. DORAIRAJ.
1970. The tunas and tuna-like fishes of India. Bull. Cent. Mar. Fish. Res. Inst. 23, 93 p.

NAKAMURA, I.
1965. Relationships of fishes referrable to the subfamily Thunninae on the basis of the axial skeleton. Bull. Misaki Mar. Biol. Inst., Kyoto Univ. 8:7-38.

NAKAMURA, I., AND S. KIKAWA.
1966. Infra-central grooves of tunas with special reference to the identification of young tunas found in the stomachs of large predators. Rep. Nankai Reg. Fish. Res. Lab. 23:55-66.

NAKAMURA, I., AND K. MORI.
1966. Morphological study on the slender tuna, *Allothunnus fallai* Serventy obtained from the Tasman Sea. Rep. Nankai Reg. Fish. Res. Lab. 23:67-83.

NAVARRO, F. D. P.
1943. La pesca de arrastre en los dondos del Cabo Blanco y del Banco Arguin (Africa Sahariana). Trab. Inst. Esp. Oceanogr. 18, 225 p.

NICHOLS, J. T., AND C. M. BREDER, JR.
1927. The marine fishes of New York and southern New England. Zoologica (N.Y.) 9:1-192.

NINNI, A. P.
1882. Sopra una forma di tonna nuova per l'Adriatico. Atti Soc. Ital. Sci. Nat. Mus. Civ. Stor. 25:261-264.

NÜMANN, W.
1955. Die Pelamiden des Schwarzen Meeres, des Bosporus, der Marmara und der Dardanellen (*Sarda sarda*). Publ. Hydrobiol. Res. Inst., Univ. Istanbul 3B:75-127.

NUNES-RUIVO, L.
1962. Copépodes parasitas de peixes das costas de Angola. (Lista faunística). Notas Mimeogr. Cent. Biol. Piscat. 33, 28 p.

OGILBY, J. D.
1887. Catalogue of the fishes of New South Wales with their principal synonyms. Fisheries of the Colony. Rep. Comm. Fish. N.S.W. 1886, Append. 6, 1-67.
1893. Edible fishes and crustaceans of New South Wales. Gov. Printer, Syd., 212 p.

OLSEN, A. M.
1962. *Allothunnus fallai* Serventy—a new record for Australian waters. Pap. Proc. R. Soc. Tasmania 96:95-96.

OSORIO, B.
1890. Estudos ichthyologicos ácerca da fauna dos dominios portuguezes na Africa. 2.a nota.—Peixes maritimos d'Angola. J. Sci. Math. Phys. Nat., Ser. 2, 5:50-60.

OTTERSTRØM, C. V.
1943. Rygstribet pelamide (*Sarda pelamis* Brünn.). Flora Fauna 49(4-5):125-126.

PADOA, E.
1967. Eggs, larva and juvenile stages of the Scombriformes (in part) of the Gulf of Naples. [In Ital.] Fauna e Flora del Golfo di Napoli 38:471-521. [Natl. Mar. Fish. Serv., Trop. Atl. Lab. Transl. 12.]

PALLAS, P. S.
1811. Zoographia Rosso-Asiatica, sistens omnium animalium in extenso Imperio Rossico et adjacentibus maribus observatorum recensionem, domicilia, mores et descriptiones, anatomen atque icones plurimorum. Petropoli, vol. 3, 428 p.

PARONA, C.
1919. Il tonno e la sua pesca. Mem. R. Com. Talassogr. Ital. Venice 68, 265 p.

PARROTT, A. W.
1958. Big game fishes and sharks of New Zealand. Hodder and Stoughton, Lond., 127 p.

PATTEN, B. G., D. T. RODMAN, AND K. D. WALDRON.
1965. The Pacific bonito *Sarda chiliensis* (Cuvier) in Puget Sound, Washington. Calif. Fish Game 51:298-299.

PELLEGRIN, J.
1908. Mission des pêcheries de la côte occidentale d'Afrique. Poissons (2e Memoire). Actes Soc. Linn. Bordeaux 62:71-102.

PEW, P.
1954. Food and game fishes of the Texas coast. Tex. Game Fish Comm., Mar. Lab. Bull. 33, Ser. IV, 68 p.

PINKAS, L.
1961. Descriptions of postlarval and juvenile bonito from the eastern Pacific Ocean. Calif. Fish Game 47:175-188.

PINKAS, L., M. S. OLIPHANT, AND I. L. K. IVERSON.
1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dep. Fish Game, Fish Bull. 152, 105 p.

POLL, M.
1947. Poissons marins. Faune de Belgique, Bruxelles, 452 p.

POSTEL, A. E.
1955. Considerations biometriques sur la denture des Cybiidés (dents maxillaires). Bull. Stn. Océanogr. Salammbo 51:57-67.

POSTEL, E.
1950. Note sur les thonidés de la presqu'ile du Cap Verte. Bull. Serv. Élev. Ind. Anim. Afr. Occ. Fr. 3(2-3):41-76.
1954. Contribution à l'étude des thonidés de l'Atlantique tropical. J. Cons. 19:356-362.
1955a. Contribution à l'étude de la biologie de quelques Scombridae de l'Atlantique tropico-oriental. Ann. Stn. Océanogr. Salammbo 10:1-167.
1955b. Contribution à l'étude des thonidés de l'Atlantique tropical (deuxième note). Rapp. P.-V. Réun., Cons. Perm. Iné. Explor. Mer 137:31-32.
1956a. Essai sur la palomette, *Orcynopsis unicolor* (Geoffroy Saint-Hilaire, 1809). Bull. Inst. Fr. Afr. Noire 18A(4):1220-1248.
1956b. Données biométriques sur quelques scombridés tunisiens. Bull. Stn. Océanogr. Salammbo 53:50-63.
1956c. Les affinités tropicales de la faune ichtyologique du golfe de Gabès. Bull. Stn. Océanogr. Salammbo 53:64-68.
1960. Liste commentée des poissons signalés dans l'Atlantique tropico-oriental nord, du Cap Spartel au Cap Roxo, suivie d'un bref aperçu sur leur répartition bathyme-

trique et geographique. Bull. Soc. Sci. Bretagne 34(3-4):241-281.

1964. Les thonides d'Afrique de Nord. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:211-220.

1973. Scomberomoridae. CLOFNAM - Check-list of the fishes of the northeastern Atlantic and of the Mediterranean. UNESCO (U.N. Educ., Sci. Cult. Organ.) 1:473-475.

POSTEL, E., P. FOURMANOIR, AND P. GUEZE.

1960. Sur quelques thons (*sensu lato*) de la Réunion, en collection au Laboratoire des Pêches Outre-Mer. Bull. Mus. Natl. Hist. Nat. Paris, Ser. 2, 32:392-394.

POTTHOFF, T.

1974. Osteological development and variation in young tunas, genus *Thunnus* (Pisces, Scombridae), from the Atlantic Ocean. Fish. Bull., U.S. 72:563-588.

1975. Development and structure of the caudal complex, the vertebral column, and the pterygiophores in the blackfin tuna (*Thunnus atlanticus*, Pisces, Scombridae). Bull. Mar. Sci. 25:205-231.

POZZI, A. J., AND L. F. BORDALE.

1935. Cuadro sistemático de los peces marinos de la República Argentina. An. Soc. Cient. Argent. 120:145-189.

QUAST, J. C.

1964. Occurrence of the Pacific bonito in coastal Alaskan waters. Copeia 1964:448.

RADOVICH, J.

1961. Relationships of some marine organisms of the Northeast Pacific to water temperatures particularly during 1957 through 1959. Calif. Dep. Fish Game, Fish Bull. 112, 62 p.

RAE, B. B., AND S. F. PIRIE.

1968. Scottish records of rare fishes-1966. Ann. Biol. 23:212.

1969. Scottish records of rare fishes-1969. Ann. Biol. 26:279.

RAFINESQUE, C.

1810. Caratteri di alcuni nuovi generi e nuove specie di animali e piante della Sicilia. San Filippo, Palermo, 105 p.

RAO, K. V. N.

1964. An account of the ripe ovaries of some Indian tunas. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:733-743.

RATHKE, H.

1837. Beitrag zur Fauna der Krym. Mém. Acad. Imp. Sci. Saint-Pétersbourg Etrang. 3:291-454.

REDEKE, H. C.

1941. De visschen van Nederland. A. W. Sijthoff, Leiden, 331 p.

RICHARDSON, J.

1846. Report on the ichthyology of the seas of China and Japan. Rep. Br. Assoc. Adv. Sci., 15th Meet., p. 187-320.

RICKER, K. E.

1959a. Mexican shore and pelagic fishes collected from Acapulco to Cape San Lucas during the 1957 cruise of the "Marijean". Univ. B.C. Inst. Fish., Mus. Contrib. 3:1-18.

1959b. Fishes collected from the Revillagigedo Islands during the 1954-1958 cruises of the "Marijean". Univ. B.C. Inst. Fish., Mus. Contrib. 4:1-10.

RISSO, A.

1810. Ichthyologie de Nice ou histoire naturelle des poissons du département des Alpes Maritimes. F. Schoell, Paris, 388 p.

1826. Histoire naturelle des poissons de la Méditerranée qui fréquentent les côtes des Alpes Maritimes, et qui vivent dans le Golfe de Nice. *In* Histoire naturelle des principales productions de l'Europe méridionale, 3:97-480. Levrault, Paris and Strasbourg.

RIVAS, L. R.

1951. A preliminary review of the western North Atlantic fishes of the family Scombridae. Bull. Mar. Sci. Gulf Caribb. 1:209-230.

1954. The pineal apparatus of tunas and related scombrid fishes as a possible light receptor controlling phototactic movements. Bull. Mar. Sci. Gulf Caribb. 3:168-180.

ROCHEBRUNE, A. T. DE.

1882. Faune de la Sénégambie. Poissons. Actes Soc. Linn. Bordeaux 36, Ser. 4, 6:23-188.

RODRÍGUEZ-RODA, J.

1966. Estudio de la bacoreta, *Euthynnus alleteratus* (Raf.), bonito, *Sarda sarda* (Bloch) y melva, *Auxis thazard* (Lac.), capturados por las almadrabas españolas. Invest. Pesq. Barc. 30:247-292.

RÖHL, E.

1942. Fauna descriptiva de Venezuela (vertebrados). Tipogr. Am. (Caracas), 431 p.

RONDELET, G.

1554. Libri de piscibus marinis. Lugdini Mathiem Bonhomme, Lyons, 583 p.

RONQUILLO, I. A.

1963. A contribution to the biology of Philippine tunas. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:1683-1752.

ROUGHLEY, T. C.

1951. Fish and fisheries of Australia. Angus and Robertson, Sydney, 343 p.

RÜPPELL, E.

1938. Neue Wirbelthiere zu der Fauna von Abyssinien gehörig. Fische des Rothen Meeres. Frankfurt am Main, 148 p.

SÁNCHEZ T., J., AND R. LAM C.

1970. Algunas características físicas y químicas de las principales especies para consumo humano y sus rendimientos en productos pesqueros, en el Perú. Inst. Mar Perú, Callao, Inf. 33, 92 p.

SANZ ECHEVERRÍA, J.

1926. Datos sobre el otolito sagita de los peces de España. Bol. R. Soc. Esp. Hist. Nat. 26(2):145-160.

SANZO, L.

1932. Uova e primi stadi larvali di *Pelamys sarda* C.V. R. Com. Talassogr. Ital. Mem. 188:3-9.

SCHMITT, W. L., AND L. P. SCHULTZ.

1940. List of the fishes taken on the Presidential Cruise of 1938. Smithson. Misc. Collect. 98(25):1-10.

SCHROEDER, W. C.

1924. Fisheries of Key West and the clam industry of Southern Florida. Rep. U.S. Comm. Fish., 1923, append. 12:1-74. (Doc. 962.)

SCHULTZ, L. P.

1960. Suborder Scombrina. Family Scombridae: Tunas. *In* L. P. Schultz, W. M. Chapman, E. A. Lachner, and L. P. Woods. Fishes of the Marshall and Marianas Islands. Bull. U.S. Nat. Mus. 202(2):410-417.

SERVENTY, D. L.

1941a. The Australian tunas. Counc. Sci. Ind. Res., Div. Fish. Rep. 104, 48 p.

1941b. Victorian tunas and some recent records. Victorian Nat. 58:51-55.

1948. *Allothunnus fallai*, a new genus and species of tuna from New Zealand. Rec. Canterbury Mus. 5:131-135.

1950. Tuna survey of north Australia. Fish. Newsl. (Aust.) 9(3):18-20.

SHEPHERD, C. E.
1910a. The "asteriscus" in fishes. Zoologist (Lond.), Ser. 4, 14(158):57-62.
1910b. Comparisons of otoliths found in fishes. Zoologist (Lond.), Ser. 4, 14(164):292-298.

SHERRIN, R. A. A.
1886. Handbook of the fishes of New Zealand. Wilsons and Horton, Auckland, 307 p.

SILAS, E. G.
1963. Synopsis of biological data on dogtooth tuna *Gymnosarda unicolor* (Rüppell) 1838 (Indo-Pacific). FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:877-899.
1964. Aspects of the taxonomy and biology of the oriental bonito *Sarda orientalis* (Temminck and Schlegel). Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:283-308.

SIVASUBRAMANIAM, K.
1967. Distribution and length-weight relationships of tunas and tuna-like fishes around Ceylon. Bull. Fish. Res. Stn. Ceylon 19(1-2):27-41.
1969. Occurrence of oriental bonito (*Sarda orientalis* Temminck and Schlegel) in the inshore waters of Ceylon. Bull. Fish. Res. Stn. Ceylon 20(1):73-77.
1970. Surface and subsurface fisheries for young and immature yellowfin tuna (*T. albacares*) around Ceylon. Bull. Fish. Res. Stn. Ceylon 21(2):113-122.

SMITH, H. M., AND T. E. B. POPE.
1906. List of fishes collected in Japan in 1903, with descriptions of new genera and species. Proc. U.S. Natl. Mus. 31:459-499.

SMITH, J. L. B.
1949. The sea fishes of southern Africa. Central News Agency, Ltd., South Africa, 550 p.
1956. The fishes of Aldabra. Part V. Ann. Mag. Nat. Hist., Ser. 12, 9(106):721-729.
1965. New records and descriptions of fishes from Southwest Africa. Rhodes Univ., Dep. Ichthyol. Occas. Pap. 3:13-23.

SMITH, J. L. B., AND M. M. SMITH.
1963. The fishes of Seychelles. Rhodes Univ., Dep. Ichthyol., Grahamstown, S. Afr., 215 p.

SMITT, F. A.
1892. A history of Scandinavian fishes by B. Fries, C. U. Ekström, and C. Sundevall. 2nd ed. revised and completed by F. A. Smitt. Part 1. P. A. Norstedt and Söner, Stockh., 566 p.

ŠOLJAN, T.
1963. Fishes of the Adriatic. Fauna et Flora Adriatica, volume 1, Pisces. Publ. for Dep. Inter. and Natl. Sci. Found., Wash., D.C. by Nolit Publ. House, Belgrade, Yugosl., 428 p.

SPRINGER, S., AND H. R. BULLIS, JR.
1956. Collections by the *OREGON* in the Gulf of Mexico. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 196, 134 p.

STANBURY, P. J.
1969. Type specimens in the Macleay Museum, University of Sydney. I. Fishes. Proc. Linn. Soc. N.S.W. 93:203-210.

STARKS, E. C.
1906. On a collection of fishes made by P. O. Simons in Ecuador and Peru. Proc. U.S. Natl. Mus. 30:761-800.
1910. The osteology and mutual relationships of the fishes belonging to the family Scombridae. J. Morphol. 21:77-99.

STASSANO, E.
1890. La pesca sulle spiagge atlantiche del Sahara. Ann. Agrar. Roma 1890:7-59.

STEAD, D. G.
1906. Fishes of Australia: A popular and systematic guide to the study of wealth within our waters. Wm. Brooks and Co., Ltd., Sydney, 278 p.
1908. The edible fishes of New South Wales: Their present importance and their potentialities. Gov. Printer, Sydney, 123 p.

STEINDACHNER, F.
1865. Vorläufiger Bericht über die an der Ostküste Tenerife's bei Santa Cruz gesammelten fische. Sitzber. Akad. Wiss. Wien 51(1):398-404.
1868. Ichthyologischer Bericht über eine nach Spanien und Portugal unternommene Reise. V. Übersicht der Meeresfische an den Küsten Spanien's und Portugal's. Sitzber. Akad. Wiss. Wien 57:351-424.

STEINDACHNER, F., AND L. DÖDERLEIN.
1884. Beiträge zur Kenntniss der Fische Japan's [III]. Denkschr. Akad. Wiss. Wien 49:171-212.

STILLMAN, C. K.
1921. A reconstructed fish. Bull. Am. Game Prot. Assoc. 10(1):15.

STORER, D. H.
1855. A history of the fishes of Massachusetts. Mem. Am. Acad. Arts Sci., New Ser., 5:122-168.

SVETOVIDOV, A. N.
1964. The fishes of the Black Sea. [In Russ.] Zool. Inst. Akad. Nauk, Opred. Faune SSSR 86:552 p.

TALBOT, F. H.
1960. Additions to the South African Museum collections of marine fishes. Ann. S. Afr. Mus. 45:257-259.
1964. The South African tunas. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:187-209.
1965. A description of the coral structure of Tutia Reef (Tanganyika Territory, East Africa), and its fish fauna. Proc. Zool. Soc. Lond. 145:431-470.

TEMMINCK, C. J., AND H. SCHLEGEL.
1844. Pisces. *In* P. F. von Siebold, Fauna Japonica . . . 1823-30, Part 3, p. 73-112. Lugduni Batavorum.

THOMAS, P. T., AND M. KUMARAN.
1963. Food of Indian tunas. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:1659-1667.

TINKER, S. W.
1944. Hawaiian fishes. Tongg Publ. Co., Honolulu, 404 p.

TIRANT, G.
1885. Notes sur les poissons de la Basse-Cochinchine et du Cambodge. Excur. Reconnais. Cochinchine Française 9:413-438 and 10:91-198. Repr. 1929, Serv. Océanogr. Pêch Indochine, Stn. Mar. Cauda, Note 6:43-163.

TOMINAGA, Y.
1966. On two tuna-like fishes captured in waters at about 40°S Lat. [In Jap., Engl. summ.] Jap. J. Ichthyol. 14:41-48.

TORTONESE, E.
1939. Risultati ittiologici del viaggio di circumnavigazione del globo della R. N. "Magenta" (1865-68). Boll. Mus. Zool. Anat. Comp. Univ. Torino 47, Ser. 3, 100:177-421.
1949. Identificazione di due Sgombroide (pesci) accidentali nel Mediterraneo. Boll. Zool. Torino 16(1-3):61-66.

1956. Brevi considerazioni sui pesci Mediterranei del Sottordine Sgombroidi. Boll. Inst. Mus. Zool. Univ. Torino 5(3):3-11.

1963. Catalogo dei tipi di pesci del Museo Civico di Storia Naturale de Genova (Parte III). Ann. Mus. Civ. Stor. Nat. Genova 73:333-350.

TORTONESE, E., AND L. TROTTI.

1949. Catalogo dei pesci del Mare Ligure. Atti Accad. Ligure Sci. Lett. 6(1):1-118.

TRETIAKOV, D. K.

1939. Olfactory organ in *Sarda sarda* C. V. Dokl. Akad. Nauk SSSR 22(4):202-205.

UEYANAGI, S.

1969. Observations on the distribution of tuna larvae in the Indo-Pacific Ocean with emphasis on the delineation of the spawning areas of albacore, *Thunnus alalunga*. [In Jap., Engl. synop.] Far Seas Fish. Res. Lab. Bull. 2:177-256.

VALENCIENNES, A.

1844. Ichthyologie des îles Canaries. *In* P. B. Webb and S. Berthelot, Histoire Naturelle des îles Canaries, Vol. 2, 109 p.

VERANY, J. B.

1847. Aggiunta al catalogo de'pesci della Liguria. Atti Sci. Ital. Genova 8:492-494.

VILDOSO, A. C. DE.

1960. Estudios sobre la reproducción del "bonito" *Sarda chilensis* (C. y V.) en aguas adyacentes a la costa peruana. Ser. Divulg. Cient. Perú 14:1-75.

1963a. Estudios sobre la reproducción del bonito *Sarda chilensis* (C. y V.) en aguas adyacentes a la costa peruana. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:1143-1152

1963b. Especies del genero *Sarda* en el Pacifico oriental. FAO (Food Agric. Organ. U.N.) Fish. Rep. 6:1549-1556.

VINCIGUERRA, D.

1890. Intorno ad alcune specie di pesci raccolte dal dottore Enrico Stassano presso la costa occidentale del Sahara. Ann. Agrar. Roma 1890:61-103.

1893. Catalogo dei pesci delle Isole Canarie. Atti Soc. Ital. Sci. Nat. Milan 34:295-334.

VLADYKOV, V. D.

1935. Some unreported and rare fishes for the coast of Nova Scotia. Proc. Nova Scotia Inst. Sci. 19(1):1-8.

WAITE, E. R.

1904. A synopsis of the fishes of New South Wales. Mem. NSW Nat. Club 2:59 p.

WALFORD, L. A.

1936. On the bonitos (*Sarda*) of the Pacific Ocean. St. Barbara Mus. Nat. Hist., Occas. Pap. 4(3):8-10.

1937. Marine game fishes of the Pacific coast from Alaska to the equator. Univ. Calif. Press, Berkeley, 205 p.

WARASHINA, I., AND K. HISADA.

1972. Geographical distribution and body length composition of two tuna-like fishes, *Gasterochisma melampus* Richardson and *Allothunnus fallai* Serventy, taken by Japanese tuna longline fishery. [In Jap., Engl. synop.] Far Seas Fish. Res. Lab. Bull. 6:51-74.

WARFEL, H. E.

1950. Outlook for development of a tuna industry in the Philippines. U.S. Fish Wildl. Serv., Res. Rep. 28, 37 p.

WATANABE, H., M. YUKINAWA, S. NAKAZAWA, AND S. UEYANAGI.

1966. On the larva probably referrable to slender tuna, *Allothunnus fallai* Serventy. [In Jap., Engl. summ.] Rep. Nankai Reg. Fish. Res. Lab. 23:85-94.

WEBB, B. F., AND D. C. WOLFE.

1974. Commercial catches of slender tuna in Tasmanian waters. Aust. Fish. 33(8):5-7.

WENT, A. E. J.

1968. Rare fishes taken in Irish waters in 1967. Ir. Nat. J. 16(2):35-39.

1969. Rare fishes taken in Irish waters in 1968. Ir. Nat. J. 16(6):147-150.

1971. Interesting fishes from Irish waters in 1970. Ir. Nat. J. 17(2):41-45.

WHEELER, A., AND R. W. BLACKER.

1969. Rare and little-known fishes in British seas in 1966 and 1967. J. Fish. Biol. 1:311-331.

1972. Rare and little-known fishes in British seas in 1968 and 1969. J. Fish. Biol. 4:141-170.

WHITLEY, G. P.

1935. Studies in ichthyology. No. 9. Rec. Aust. Mus. 19:215-250.

1936. More ichthyological miscellanea. Mem. Queensl. Mus. 11:23-51.

1939. Studies in ichthyology. No. 12. Rec. Aust. Mus. 20:264-277.

1945. New sharks and fishes from Western Australia. Part 2. Aust. Zool. 11(1):1-42.

1947. New sharks and fishes from Western Australia. Part 3. Aust. Zool. 11(2):129-150.

1948. A list of the fishes of Western Australia. W. Aust. Fish. Dep., Fish. Bull. 2, 35 p.

1964a. Scombroid fishes of Australia and New Zealand. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India, Symp. Ser. 1:221-253.

1964b. A survey of Australian ichthyology. Proc. Linn. Soc. N.S.W. 89:11-127.

1968. A check-list of the fishes recorded from the New Zealand region. Aust. Zool. 15(1):102 p.

WILLIAMS, F.

1964. The scombroid fishes of East Africa. Proc. Symp. Scombroid Fishes. Mar. Biol. Assoc. India. Symp. Ser. 1:107-164.

1968. Report on the Guinean Trawling Survey. Volume I. Gen. Rep. Org. Afr. Unity, Sci., Tech. and Res. Comm., Lagos, Nigeria. OAU/STRC Publ. 99, 828 p.

WILLUGHBY, F.

1686. Historia piscium libri quatuor . . . Totum opus recog novit, coaptavit, supplevit, librum etiam prjmum et secundum integors adjecit Johannes Raius. Oxonii, 343 p.

ZHAROV, V. L.

1967. Classification of scombroid fishes (Suborder Scombroidei, Order Perciformes). [In Russ.] Vopr. Ikhtiol. 43:209-224. (Transl. Natl. Mar. Fish. Serv. Hawaii Area Fish. Cent.)

VELOCITY AND TRANSPORT OF THE ANTILLES CURRENT NORTHEAST OF THE BAHAMA ISLANDS

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ABSTRACT

Meridional geostrophic velocities and volume transports were computed from data collected on six occupations of Standard Section A-7 by U.S. Coast Guard cutters. The section extends offshore from Cape Canaveral, Fla., along lat. 28°35'N for about 520 nautical miles (960 km), but this study involved only that portion seaward of the 800-m isobath (situated at about long. 79° 30'W), a portion which would transect the Antilles Current just before it merges with the Gulf Stream. The velocity sections did not reveal a broad northward flowing Antilles Current in the surface layer as has been shown on many average current charts in the past. Instead, the sections revealed a generally sluggish (≤10 cm/s) surface flow, either northward or southward. Imbedded in the low speed surface flow were two bands of higher speed (10-40 cm/s), one northward and the other southward, usually located in the vicinity of the 1,000-fathom (1,830-m) isobath. Computed net transport for the sections ranged from 30.4×10^6 m³/s northward to 6.4×10^6 m³/s southward, with an average of 8.6×10^6 m³/s northward, which is considerably less than customarily hypothesized in the past to provide for the observed downstream increase in Gulf Stream transport between the Straits of Florida and Cape Hatteras, N.C.

The position of the band of relatively rapid southward flow corresponded approximately with the position suggested by Kort for the southward flowing Antilles-Guiana Countercurrent. A comparison of temperature-salinity properties in the bands showed them to be identical with each other but different from Florida Current water, making it highly unlikely that the bands are manifestations of two continuous currents, the Antilles Current and Antilles-Guiana Countercurrent, from different source areas. The identical temperature-salinity properties of the bands indicate that they are manifestations of eddies or a countercurrent formed by recurving of an adjacent current; the former alternative appears more likely.

The importance of the Antilles Current as a means of transporting significant quantities of pelagic ichthyoplankton into the Gulf Stream system is doubtful. The current speeds and transports appear to be substantially less than hypothesized and highly variable. An alternate means of transport of ichthyoplankton in the surface layer which may be in operation is Ekman drift generated by local winds, yielding a flow which may not be reflected in the field of mass and geostrophic computations.

One of the objectives of the initial ichthyoplankton cruises of the MARMAP (Marine Resources Monitoring Assessment and Prediction) program of the National Marine Fisheries Service was to estimate the transport of eggs and larvae of pelagic fishes into the Gulf Stream system by the Antilles Current. Scientists in the program began gathering information and data from various sources in an attempt to characterize the Antilles Current and other currents in the area of interest, the western North Atlantic and northern Caribbean Sea. These attempts revealed that the portion of the Antilles Current east of the Bahama Islands and northward has been little investigated and is only sketchily described, even though frequently mentioned in general works and shown on charts of "average" or "permanent" surface currents. Descriptions based on ship-drift data (U.S. Naval Oceanographic Office 1965; Boisvert 1967) portray the surface current in this region as having a prevailing direction of flow toward the north-northwest with a modal speed of about 0.5 knot (25 cm/s), an average speed of about 0.7 knot (35 cm/s), and a directional persistence of 40-55% in most of the area, except immediately north of the Bahama Islands, where a pair of eddies are shown (Figure 1). The strongest currents were found in a narrow band 10-30 nautical miles (18-55 km) wide near the Bahama Banks.

The junction of the Antilles Current with the Gulf Stream generally has been thought to occur over about 8° of latitude south of Cape Hatteras, N.C., (about lat. 28°-36°N) with the current supposedly adding about 60×10^6 m³/s to the transport of the Gulf Stream, approximately tripling its flow (Stommel 1965). Knauss (1969) concluded from direct and indirect measurements of Gulf Stream transport in the Florida Straits-Cape Hatteras area that there is a gradual, uniform addition of

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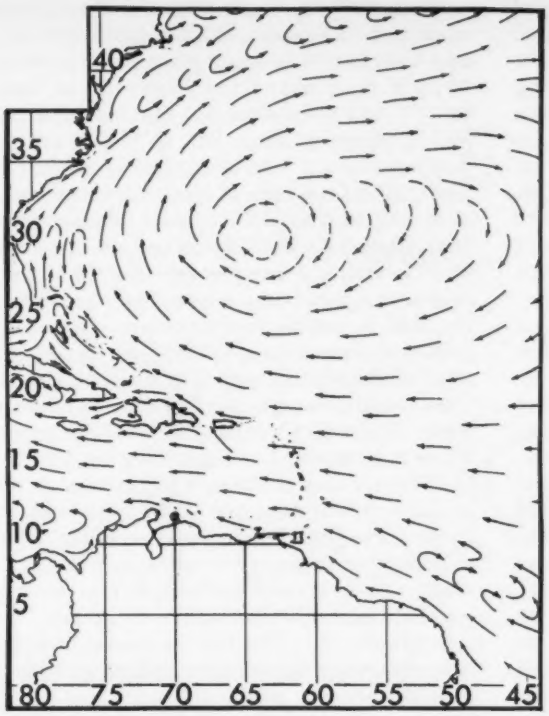

FIGURE 1.–Surface currents in the western North Atlantic and Caribbean during the winter months (from Oceanographic Atlas of the North Atlantic Ocean. Section I. Tides and currents. U.S. Nav. Oceanogr. Off. Publ. 700).

volume to the Gulf Stream at the rate of 7% per 100 km of its path leading to total values off Cape Hatteras of about 60×10^6 m^3/s. Knauss did not speculate on the source of the water added to the Gulf Stream. More recent direct measurements of the transport of the Gulf Stream off Cape Hatteras (Richardson and Knauss 1971) yielded an average value of 63×10^6 m^3/s which means that the addition to the Gulf Stream between the Florida Straits and Cape Hatteras, assumedly from the Antilles Current, amounts to about 30×10^6 m^3/s, approximately doubling its flow.

Some doubt has been cast on the existence of the hypothesized junction of the Antilles Current with the Gulf Stream and even on the existence of the current itself. A study by Day (1954) of drift bottle data and hydrographic data then available from the region northeast of the Bahama Islands revealed little evidence of a surface current with the characteristics attributed to the Antilles Current. Instead of surface flow to the northwest, he found that "... the surface waters in the region tend to move with a pronounced southerly component of direction rather than to the northwest, and that the Antilles Current appears at depth, varies markedly in its transport from one time to another, and should not be considered a permanent, clearly defined tributary to the Gulf Stream current." A hydrographic section occupied between Bermuda and Elbow Cay in the northern Bahamas in February 1933 showed a northwestward transport of 20.3×10^6 m^3/s in a 140-nautical mile band off Elbow Cay (lat. 26° 30′N) which Day identified as the Antilles Current.

Earlier, Iselin (1936) commented on this same section of stations, pointing out that: 1) the temperature field was nearly horizontal except near the Bahamas (within 40 nautical miles) where it indicated southward flow in the upper 400 m and northward flow beneath that; 2) the temperature observations showed no evidence of a "... broad or powerful Antilles Current, readily distinguishable from the general westerly movement continuing from the Northern Equatorial Current . . ."; 3) salinity observations agreed with the thermal trends and afforded little further evidence for the Antilles Current; and 4) at other times of the year, when the trade winds are stronger, the Antilles Current may be better developed.

Day (1954) also points out that a dynamic

topography based on a grid of stations occupied northeast of the Bahama Islands in April 1947 showed no general manifestations of the Antilles Current in the upper 150 m, showing southeastward flow instead. In a 330-nautical mile (610-km) section from this grid off Great Abaco Island (about lat. 27° to 28°N), a southeastward flow of 2.8×10^6 m^3/s was found in the upper 250 m, and a weak northwestward flow of 0.7×10^6 m^3/s was found in the 250- to 1,000-m layer, yielding a net transport through the section of 2.1×10^6 m^3/s southeastward.

A similar conclusion can be drawn concerning a much earlier investigation. Although Bigelow (1917), in his pioneer analysis of the *Bache* data, regarded the northward extension of warm water in the surface layer east and north of the Bahama Islands to be an expression of the Antilles Current, his pertinent vertical section of temperature just north of the Bahamas collected in March 1914 doesn't support that contention. The slope of the temperature isopleths northeast of the Bahama Islands indicated the presence of a southward flowing surface current in the upper 200 m or so, with a northward current at greater depth. Wüst (1924) computed geostrophic current speeds and volume transports from the *Bache* data including the transect of eight stations, from Jupiter Inlet to the Sargasso Sea (SW-NE) crossing just north of the Bahamas. He found an 80-km band of northwestward flow, which he called the Antilles Current, contiguous with southeastward flowing countercurrents on both sides. The transport of the Antilles Current he computed, 12.0×10^6 m^3/s, was approximately balanced by the transport of the two countercurrents, 12.4×10^6 m^3/s, yielding a net transport through the portion of the section seaward of the Gulf Stream (depths>800-900 m) of 0.4×10^6 m^3/s to the southeast.

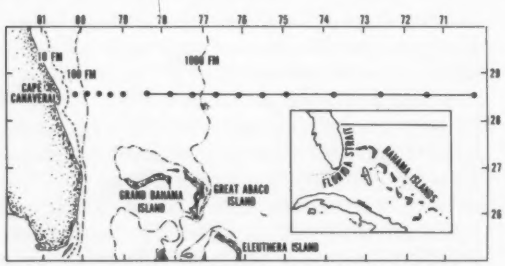

FIGURE 2.–Location of stations occupied by U.S. Coast Guard cutters along Standard Section A-7. The stations connected by the solid line are those generally used in this study.

During 1967-72, vessels of the U.S. Coast Guard made nine occupations of Standard Section A-7, each consisting of 16 oceanographic stations along 28°35′N from near Cape Canaveral at long. 80°10′W to a point about 520 nautical miles (960 km) offshore at long. 70° 15′W (Figure 2). Temperature and salinity data were collected on each station from casts of Nansen bottles located at or near NODC (U.S. National Oceanographic Data Center) standard depths or from lowerings of STD (Salinity Temperature Depth) sensors calibrated against data collected by Nansen bottles and reversing thermometers. Contoured profiles of temperature, salinity, and density are to be published along with lists of the data in the Coast Guard Oceanographic Report series (Robe in press). This section transects the Antilles Current where it is supposed to begin merging with the Gulf Stream, thus providing a portrayal of its potential contribution to the Gulf Stream system. Unfortunately, the occupations are not distributed uniformly throughout the seasons; five are in winter, two in fall, and two in summer, so seasonal variations cannot be discerned from the data.

Geostrophic velocities were computed from the temperature and salinity data utilizing a standard computer program employed by the Coast Guard Oceanographic Unit (Hislop[2]). The velocities were computed relative to the 1,000-decibar surface which was consistently reasonably level, as indicated by the small variation of density at 1,000 m (mean σ_t = 27.547, standard deviation = 0.098, sample size = 52). No attempt was made to carry the computation into water shallower than about 800 m because of the considerable errors introduced by extrapolation of water properties into the bottom and by close approach to the Gulf Stream.

Vertical sections of geostrophic velocity were hand drawn from lists of the computed values by assigning the values to midpoints between stations at middepths between depths of temperature and salinity observations. Interpolations necessary for contouring were based on an assumption of linear variation in properties horizontally and vertically between data points. This procedure was followed for six of the nine occupations of Standard Section A-7. Three occupations were rejected because they contained too many short casts in critical areas.

[2]Hislop, A. S. 1973. Coast Guard Oceanographic Unit DDP-516 programs. Oceanogr. Unit Tech. Rep. 73-2, p. 16-17. Unpubl. manuscr.

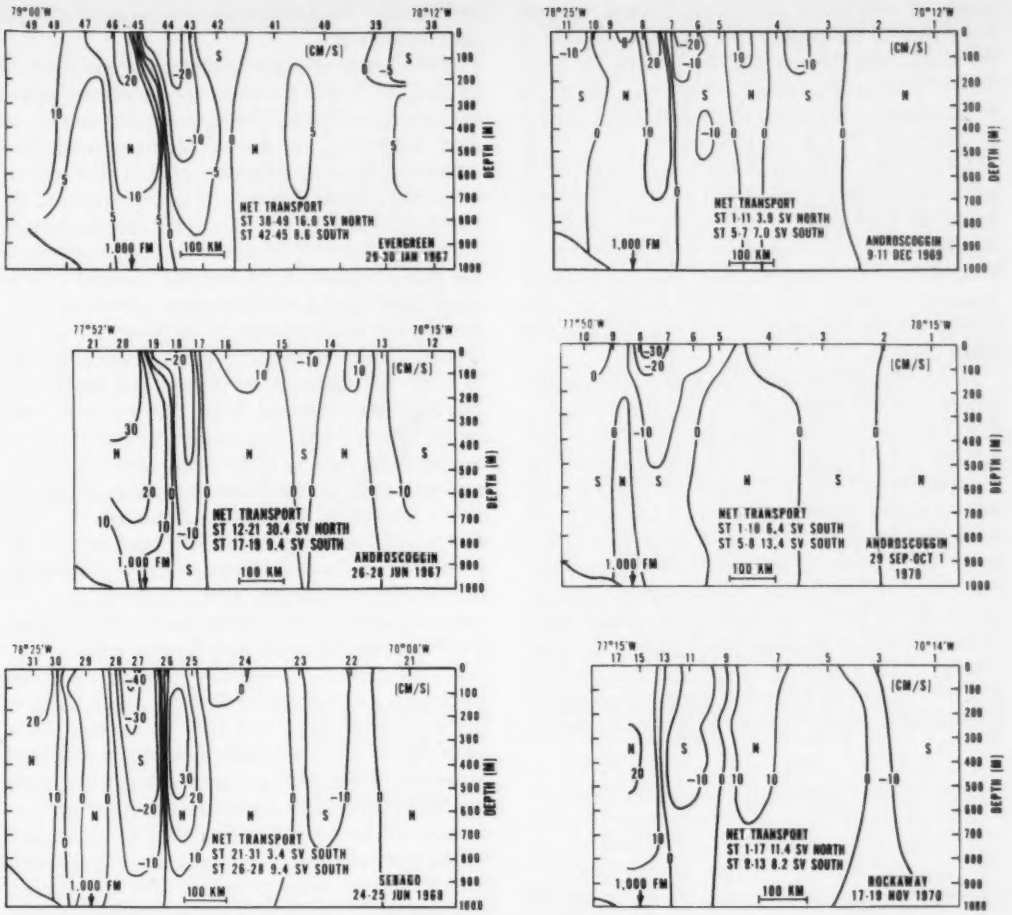

FIGURE 3.—Vertical distributions of meridional geostrophic velocity (cm/s) through Standard Section A-7 computed relative to the 1,000-decibar surface. Net transport values given in Sverdrups (1 SV = 10^6 m^3/s). Station numbers are arrayed along the upper horizontal boundary. Positive velocities are northward.

The vertical sections of geostrophic velocity (Figure 3) revealed a fairly consistent pattern of alternate bands of weak ($\leq$10 cm/s) northward and southward flow in the offshore half of the transect (seaward 400-500 km). West of this, a narrow band of stronger (10-40 cm/s) northward current was found in five of the sections, located generally just seaward of the 1,000-fathom isobath, about where the band of stronger northward Antilles Current was shown by Boisvert (1967). However, a band of southward flow of about the same speed was found nearby in each of the transects. Net transport through the section was northward in four of the occupations and southward in two, ranging from 3.9 to 30.4×10^6 m^3/s northward and 3.4 to 6.4×10^6 m^3/s southward. The mean net transport for the six sections was 8.6×10^6 m^3/s northward. In five of the sections, the northward transport values fall far short of the 30×10^6 m^3/s or more which the Antilles Current is supposed to add to the Gulf Stream, indicating that sources other than the Antilles Current must contribute to the observed increase.

Although it is difficult to make a direct comparison with Kort's findings (Kort 1972), because of the small size of his charts, paucity of data portrayed, and the fact that all of his data were collected south of lat. 28° 35'N, the locations of the

bands of relatively strong southward current corresponded reasonably well with the location of the southward flowing Antilles-Guiana Countercurrent that he hypothesized (Figure 4). Estimates of transport in the major southward band in each of the Coast Guard sections varied from 7.0 to 13.4×10^6 m³/s, with an average of 9.3×10^6 m³/s, which is only about one-third of the southward transport Kort (1972) reported for the Antilles-Guiana Countercurrent. However, Kort's value, computed for the transect near the coast of South America at about lat. 8°N, was based on data throughout the entire water column, not just the upper 1,000 m.

Kort's discussion includes some speculation concerning the source of his hypothesized Antilles-Guiana Countercurrent as follows: "One may suppose that a branch of the Florida or North Tradewind Currents is a source of the Antilles-Guiana Countercurrent. On the other hand, the studies made by Swallow and Worthington (1961) in the Gulf Stream in 1961 enable one to consider that the Antilles-Guiana Countercurrent can be traced far to the north flowing as a southward countercurrent on the oceanward side of the Gulf Stream." His portrayal of the general current pattern (Figure 4), however, shows recurving of the Florida Current, "North Tradewind Current,"

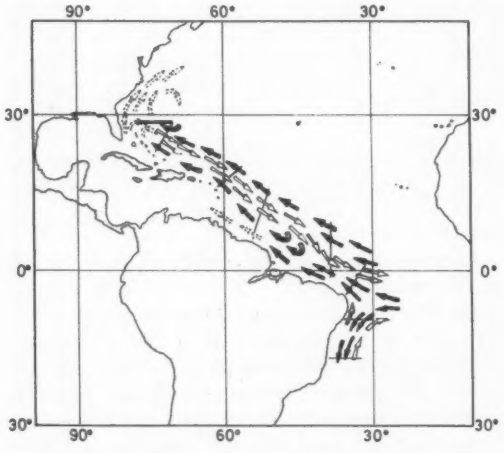

FIGURE 4.—Location of hypothesized Antilles-Guiana Countercurrent (open arrows) according to Kort (1972). Solid lines crossing the arrow field indicate locations of oceanographic transects. The northernmost, broad line represents the portion of the U.S. Coast Guard Standard Section used in this study; the others are sections cited by Kort.

and possibly the Antilles Current, as sources of the countercurrent.

If the bands of southward flowing water found in the Coast Guard transects are manifestations of the Antilles-Guiana Countercurrent and if, as Kort suggested, the source of the hypothesized Antilles-Guiana Countercurrent is (1) the recurving of the Florida Current, (2) the recurving of the North Tradewind Current, or (3) a countercurrent seaward of the Gulf Stream, then the properties of the water masses in the Antilles Current (northward band) and Antilles-Guiana Countercurrent (southward band) should be different. A plot of observed temperature and salinity values (Figure 5) from the bands of northward and southward flowing water detected in the Coast Guard transects shows that the bands have identical temperature-salinity (T-S) characteristics, implying that none of the three sources suggested is valid. Further, the comparison of the T-S characteristics of the southward band with those of the Florida Current (Figure 5) shows them to be significantly different, substantiating the contention that the recurving of the Florida Current is not a source for southward flowing water.

The identical T-S properties of the water in the southward and northward flowing bands leads to the conclusion that one flow is formed by a recurving of the other. Such recurving would lead to the formation of either a countercurrent, such as the hypothetical Antilles-Guiana Countercurrent, or an eddy. On the basis of the Coast Guard transect data it is impossible to determine which feature was present, but the direct measurement of large scale eddies farther south in the Antilles Current performed by satellite tracking of drogue buoys (Hansen[3]) suggests that eddies are more likely. The nearly constant position of the bands of northward and southward flow (eddies) in the transects would suggest that they are formed as a consequence of interaction of the Antilles Current with the Bahama Islands and surrounding banks.

The significance of these findings in relation to the distribution of ichthyoplankton in the area of the northern Antilles Current is difficult to state positively. However, it is clear that eggs and larvae in the upper 200 m in this area cannot be

[3]Hansen, D. V. Mesoscale motions in the Sargasso Sea: A result from the EOLE Complementary Program. Presented to the 54th meeting of the American Geophysical Union, April 18, 1973.

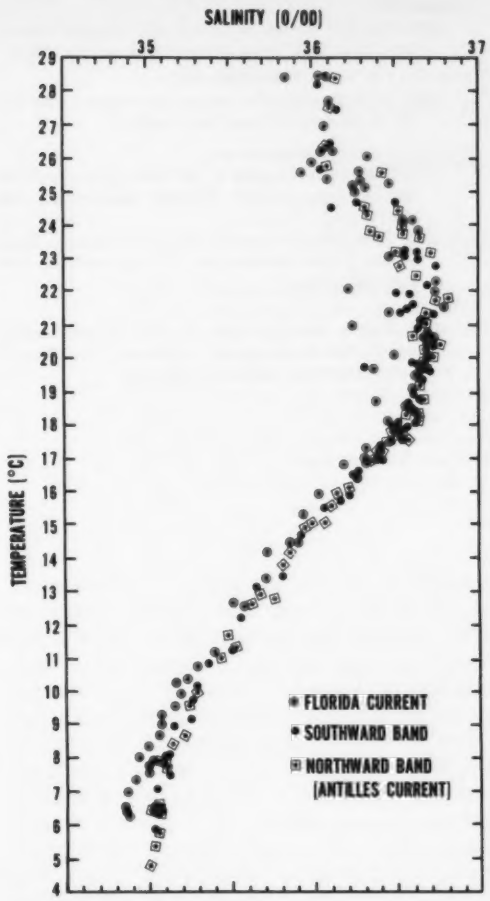

FIGURE 5.—Observed temperature (°C) - salinity (°/oo) points in the northward and southward bands and the Florida Current from six occupations of Standard Section A-7.

assumed to be moving steadily toward the northwest along the path traditionally assigned to the Antilles Current. Planktonic organisms located in water just seaward of the continental shelf at this latitude (28.5°N) are likely to have a northward compoent of velocity of about 10-30 cm/s, while those in deeper water 100-200 km farther offshore are likely to have a southward component of about the same magnitude. Seaward of that, plankton are likely to move either northward or southward at relatively slow speeds, in the range of 5-10 cm/s. If the higher speeds in the northward and southward bands are manifestations of a quasi-permanent eddy or transient eddies passing through, the net northward transport of plankton would be small, even in the area of higher current speeds near the continental shelf. Instead, planktonic organisms may be caught up in eddies or slowly moving water for long periods of time. Since the waters east of the northern Bahama Islands contain a relatively small plankton biomass and are thought to yield low rates of primary and secondary production, pelagic fish larvae held in the area for an extended period of time would have little likelihood of growth and survival.

A clearer resolution of quasi steady-state currents should be realized when analysis of data and geostrophic computations are complete for two MARMAP cruises (July-August 1972 and January-March 1973), which included the area east of the Bahama Islands. However, the transport of planktonic organisms in the surface layer may be governed by local wind-driven currents which may not be manifested as geostrophic currents computed from the density field. Average monthly wind roses (U.S. Naval Oceanographic Office 1963) for the area off the northern Bahamas shows that the winds from the east or northeast occur with greater frequency than those from any other quadrant every month, except June, July, and August, when winds from the south and southeast are more frequent. Such easterly and northeasterly winds would yield northward and northwestward Ekman (wind-driven) transports in the surface layer coinciding with the direction assumed for the Antilles Current. The net Ekman transport in the surface layer depends on the frequency distribution of wind direction and speed during the time period of interest, the subject of further research.

LITERATURE CITED

BIGELOW, H. B.
1917. Explorations of the United States Coast and Geodetic Survey steamer "BACHE" in the Western Atlantic, January-March, 1914, under the direction of the United States Bureau of Fisheries. Oceanography. U.S. Bur. Fish., Rep. U.S. Comm. Fish., 1915, append. V (Doc. 833), 62 p.

BOISVERT, W. E.
1967. Major currents in the North and South Atlantic Oceans between 64°N and 60°S. U.S. Nav. Oceanogr. Off., Tech. Rep. TR-193, 92 p.

DAY, C. G.
1954. A note on the circulation in the region northeast of the Bahama Islands. Woods Hole Oceanogr. Inst., Tech. Rep. 54-4, 6 p.

ISELIN, C. O'D.
1936. A study of the circulation of the western North Atlantic. Pap. Phys. Oceanogr. Meteorol. 4(4), 101 p.

KNAUSS, J. A.
1969. A note on the transport of the Gulf Stream. Deep-Sea Res. 16 (Suppl.):117-123.

KORT, V. G.
1972. New data on the dynamic structure of the western boundary currents in the tropical Atlantic. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 162:276-279.

RICHARDSON, P. L., AND J. A. KNAUSS.
1971. Gulf Stream and Western Boundary Undercurrent observations at Cape Hatteras. Deep-Sea Res. 18:1089-1110.

ROBE, R. O.
In press. Oceanographic observations. North Atlantic Standard Monitoring Sections A5, A6 and A7, 1967-69. U.S. Coast Guard Oceanogr. Rep. 67(CG 373-67).

STOMMEL, H.
1965. The Gulf Stream. A physical and dynamical description. Univ. Calif. Press, Berkeley and Los Ang., 248 p.

SWALLOW, J. C., AND L. V. WORTHINGTON.
1961. An observation of a deep counter current in the western North Atlantic. Deep-Sea Res. 8:1-19.

U. S. NAVAL OCEANOGRAPHIC OFFICE.
1963. Oceanographic atlas of the North Atlantic Ocean. Section IV. Sea and swell. U.S. Nav. Oceanogr. Off. Publ. 700-IV, 227 p.
1965. Oceanographic atlas of the North Atlantic Ocean. Section I. Tides and currents. U.S. Nav. Oceanogr. Off. Publ. 700-I, 75 p.

WÜST, G.
1924. Florida- und Antillenstrom. Eine Hydroynamische Veroff. Untersuchung. Inst. Meeresk. Univ. Berl. A. Geogr.-naturwiss. Reihe. Heft 12, 48 p.

THE DISTRIBUTION OF MYCTOPHID FISHES ACROSS THE CENTRAL EQUATORIAL PACIFIC

A. RUCKER HARTMANN[1] AND THOMAS A. CLARKE[2]

ABSTRACT

Analysis of myctophid fishes collected in the upper 50-75 m at night along long. 145°W between lat. 12°N and 3°30'S indicated three faunal groups. Warmwater species ocurred across the entire transect and were most abundant at or just north of the equator. A second group of species occurred only in the North Equatorial Current or the Counter Current, but most are known to be more widely distributed. A third group occurred only at or just north of the equator; all are apparently found within a small latitudinal range between about long. 130° and 170°W. Certain species which are abundant in the central water mass were absent from the present samples. The faunal change within the equatorial water mass is likely a response to the increased primary production and food supply resulting from upwelling near the equator and northward transport of enriched surface waters. Some of the faunal changes observed appear to be replacements of one species by a congener or morphologically similar species.

The geographic ranges of oceanic organisms frequently conform with the boundaries of the major water masses (Johnson and Brinton 1963). The water masses are, however, large-scale, subsurface features defined by the temperature-salinity profiles of the deeper water (Sverdrup et al. 1942). In the surface layers of a given water mass there are variations in temperature and salinity as well as in other biologically relevant factors. Thus it is not surprising that, within major water masses, subpatterns of abundance and distribution have been reported for species which might likely respond to such variations in the upper layers. There are numerous reports of subpatterns in epipelagic zooplankton, e.g., Fager and McGowan (1963) and McGowan (1971); and Ebeling (1962) and Backus et al. (1969) have noted similar changes within water masses for mesopelagic fishes. Backus et al. related these to shallow thermal fronts, and Ebeling suggested that, where species' ranges deviated from water-mass boundaries, they were related to variation in primary productivity in the surface layers.

Within the Pacific equatorial water mass, major and presumably biologically relevant changes are observed in the upper layers. Grandperrin and Rivaton (1966), studying the mesopelagic fishes along the equator, found four longitudinal faunal zones which appeared related to the depth of the Cromwell Current or Equatorial Undercurrent, variations in primary productivity, and concentrations of dissolved oxygen and nutrients in the upper layers. Latitudinally, one encounters four separate current regimes in the upper layers (Cromwell 1951) with associated changes in thermocline depths. Marked changes in primary productivity (Koblentz-Mishke et al. 1970), zooplankton volume (King and Hida 1957), and tuna abundance (Murphy and Shomura 1972) also occur across the water mass.

This study considers the distribution and abundance of myctophid fishes collected by shallow night trawl tows across a latitudinal transect of the Pacific equatorial water mass. It was expected that any patterns observed might be related to available data on differences in surface layer features.

MATERIALS AND METHODS

Most data were collected during cruise 43 of the U.S. Fish and Wildlife Service RV *Townsend Cromwell* (29 April-11 June 1969). Pelagic trawl collections were made along long. 145°W at five latitudes: approximately 12°N, 7°30'N, 3°30'N, 0°, and 3°30'S. Five tows were made with a modified Cobb pelagic trawl (CT) described by Higgins

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(1970) at each latitude except lat. 3°30'S (four tows). Towing speed was about 2 knots (ca. 1 m/s). All tows were made at night; the trawl was at depth for about 6 h each tow (2000-0200 h). Depths of tows were estimated from amount of wire out, wire angle, and depth determinations made on later cruises with a time-depth recorder. Two depth zones were sampled–20-30 m and 50-75 m. These will be referred to as "shallow" and "deep" tows, respectively. Depth of tow was alternated nightly except at the equator where all tows were deep. Station numbers, exact positions, depths, and dates are given in Table 1.

TABLE 1.–Station numbers, positions, towing depths, and dates of mid-water trawl collections taken May-June 1969 on cruise 43 of the RV *Townsend Cromwell*.

Station number	Position		Depth (m)	Date
	Lat.	Long.		
8	12°04′ N,	144°54′ W	20-30	7 May
10	12°03′ N,	144°55′ W	50-75	8 May
12	12°11′ N,	145°11′ W	20-30	9 May
14	11°56′ N,	144°54′ W	50-75	10 May
16	11°58′ N,	144°57′ W	20-30	11 May
22	07°41′ N,	145°01′ W	50-75	13 May
24	07°27′ N,	145°05′ W	20-30	14 May
26	07°33′ N,	144°50′ W	50-75	15 May
28	07°33′ N,	144°48′ W	20-30	16 May
30	07°19′ N,	145°09′ W	50-75	17 May
36	03°29′ N,	145°03′ W	20-30	19 May
38	03°30′ N,	145°06′ W	50-75	20 May
40	03°31′ N,	145°00′ W	20-30	21 May
42	03°32′ N,	144°59′ W	50-75	22 May
44	03°40′ N,	144°54′ W	20-30	23 May
46	00°01′ N,	144°50′ W	50-75	25 May
48	00°04′ N,	145°07′ W	50-75	26 May
50	00°03′ N,	145°05′ W	50-75	27 May
52	00°01′ N,	145°03′ W	50-75	28 May
54	00°04′ N,	144°59′ W	50-75	29 May
55	02°59′ S,	144°53′ W	20-30	30 May
57	03°31′ S,	145°11′ W	50-75	31 May
59	03°34′ S,	145°00′ W	20-30	1 June
61	03°35′ S,	145°11′ W	50-75	2 June

Except for very large samples, the entire collection was preserved and counted. When total volume of the sample exceeded ca. 4 gallons (ca. 15 liters), 1-gallon (ca. 4 liters) subsamples were preserved, and counts were adjusted according to the original total volume. Specimens were identified primarily from Nafpaktitis (1968), Nafpaktitis and Nafpaktitis (1969), and an unpublished manuscript kindly provided by R. L. Wisner.[3]

During cruise 43, bathythermograph casts to 300 m were made at approximately 50-km intervals between lat. 14° and 3°N and at approximately 16-km intervals between lat. 3°N and 3°S. Salinity-temperature-depth casts to 500 m were made every degree from lat. 14° to 3°N and every 32 km from lat. 3°N to 3°S.

We have also counted the myctophids from 12 tows with a 10-foot (3 m) Isaacs-Kidd mid-water trawl (IK) taken 5-11 February 1970 at lat. 3°30'N, long. 145°W during cruise 47 of the *Townsend Cromwell*. These tows were all taken at night. Towing depths were 50-500 m; each tow spent about 2 h at depth (Table 2). The data from these tows along with data on vertical distribution of myctophids near Hawaii, somewhat north and west of the sampling area (Clarke 1973), allow us to estimate whether the absence of certain species from Cobb trawl tows in some zones was due to the species' simply occurring deeper than the Cobb trawl sampled.

TABLE 2.–Station numbers, towing depths, and dates of mid-water trawl collections taken near lat. 3°30'N, long. 145°W, February 1970 on cruise 47 of the RV *Townsend Cromwell*.

Station number	Depth (m)	Date
48	50	5 Feb.
49	50	5 Feb.
52	450	6 Feb.
57	200	7 Feb.
58	100	7 Feb.
60	500	7 Feb.
61	300	8 Feb.
67	300	9 Feb.
68	100	10 Feb.
69	200	10 Feb.
76	450	10 Feb.
78	500	11 Feb.

RESULTS AND DISCUSSION

The slope of the isotherms on the temperature profile of the transect (Figure 1) indicate the locations of the major currents of the area. The North Equatorial Current (NEC) extended to about lat. 9°N, the Equatorial Counter Current (ECC) from about lat. 4° to 9°N, and the South Equatorial Current (SEC) southward from about lat. 4°N. The Cromwell Current or Equatorial Undercurrent (EUC) was centered about on the equator. Thus the lat. 12°N samples were taken within the NEC, the lat. 7°30'N samples just south of the boundary between the NEC and the ECC, and the other samples in the SEC, the lat 0° samples actually being in the upper layers of the EUC.

A total of 32 species of myctophids were taken by the CT collections. The catches per tow are given in Table 3. Failure to catch a given species at

[3]Wisner, R. L. Annotated and illustrated key to the identification of fishes of the family Myctophidae of the eastern Pacific Ocean, eastward of 160° West Longitude. Unpubl. manuscr., Scripps Institution of Oceanography, La Jolla, CA 92037.

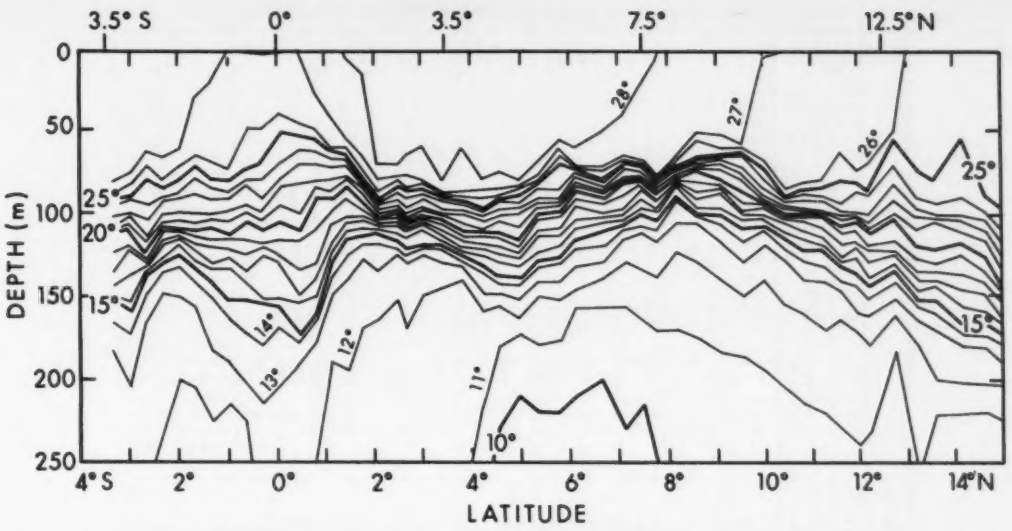

FIGURE 1.—Temperature (in degrees Celsius) profile along long. 145°W. (Compiled by R. A. Barkley from data collected on cruise 43 of the RV *Townsend Cromwell*.)

all stations at a given latitude does not, of course, necessarily mean the species was not present. It may have been present at low abundance and missed by the collections or may have occurred at depths greater than 75 m. With respect to the first possibility, we have ignored zero values in a few cases below, e.g., for very rare species and for the data from lat. 3°30′S where total catches were so much lower than elsewhere that it is likely some fraction of the total species present were not caught. With respect to the second possible source of error, we exclude from further consideration six species for which the upper limit of the depth range is close to the depth of the deep CT tows. Based on vertical distribution data from near Hawaii (Clarke 1973), only slight changes in the depth ranges of *Diaphus brachycephalus*, *Notolychnus valdiviae*, and *Lampanyctus steinbecki* would determine presence or absence in the CT collections. The IK data from lat. 3°30′N (Table 4) indicates that the same may be true for *D. jenseni*, *D. longleyi*, and *D. splendidus*. In the absence of data to the contrary and in some cases with reasonable evidence (see below), we assume that the remaining 26 species have shallow nighttime depth ranges wherever they occur in any abundance and that zero catches were not the result of changes in depth ranges with latitude.

In the presentation below, we attempt to relate patterns of distribution in the study area to other data on the species. Unfortunately, we have felt it necessary to disregard data from certain earlier studies where species identifications are doubtful. We have relied heavily on data from recent studies by Clarke (1973) near Hawaii, by M. A. Barnett (pers. commun.) near the center of the eastern central Pacific gyre (ca. lat. 29°N, long. 155°W), and by Ahlstrom (1971, 1972) in the eastern equatorial Pacific. For convenience, these will not be cited formally each time; unless otherwise cited, "near Hawaii," "gyre center," and "eastern equatorial," respectively, refer to the above three studies.

Eight species occurred across the entire sampling area. These were: *Hygophum proximum*, *Diogenichthys atlanticus*, *Myctophum aurolaternatum*, *M. spinosum*, *Symbolophorus evermanni*, *Diaphus fragilis*, *Triphoturus nigrescens*, and *Ceratoscopelus warmingi*. Other records of these species and of *M. nitidulum* and *Bolinichthys longipes*, which were taken at all latitudes except 3°30′S, indicate that all 10 occur widely throughout central water masses of the Indo-Pacific and, in most cases, the world (Bekker 1965; Nafpaktitis 1968; Nafpaktitis and Nafpaktitis 1969; Gibbs et al. 1971; Wisner footnote 3). All but *M. aurolaternatum* are taken consistently near Hawaii and all have been taken at the gyre center.

TABLE 3.—Species of myctophids and number taken per tow for stations given in Table 1. Stations are grouped by latitude and by depth (Shallow = 20-30 m, Deep = 50-75 m). Species are grouped in roughly the order considered in the text.

Species	Lat. 12°N					Lat 7°30'N					Lat. 3°30'N					Lat. 0°					Lat. 3°30'S			
	Shallow			Deep		Shallow		Deep			Shallow			Deep		Deep					Shallow		Deep	
	Stn. 8	12	16	10	14	24	28	22	26	30	36	40	44	38	42	46	48	50	52	54	55	59	57	61
Diaphus brachycephalus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	21	2	1
Diaphus jenseni	—	—	—	—	—	—	—	—	—	—	—	—	—	53	46	7	5	11	4	60	—	—	—	—
Diaphus longleyi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—
Diaphus splendidus	—	—	—	—	—	—	—	—	1	106	—	—	11	—	—	—	—	—	—	—	—	—	—	—
Notolychnus valdiviae	—	—	—	—	—	—	—	—	—	—	—	—	—	4	2	312	4	—	12	144	—	—	—	13
Lampanycytus steinbecki	—	—	—	—	20	—	—	—	—	26	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hygophum proximum	8	—	3	170	30	111	51	206	274	98	17	58	52	35	26	91	40	176	64	196	55	117	175	157
Diogenichthys atlanticus	—	—	—	9	1	—	—	5	7	12	1	—	14	60	52	26	4	22	12	32	—	2	27	19
Myctophum aurolaternatum	4	1	1	1	1	3	1	10	18	14	8	5	8	20	16	12	14	20	6	8	1	1	0	0
Myctophum spinosum	1	—	—	—	—	12	1	14	4	10	4	24	6	3	5	5	7	55	48	20	—	1	—	—
Symbolophorus evermanni	1,491	334	270	62	75	446	745	514	359	927	92	141	161	220	92	1,216	819	968	1,984	1,244	43	4	75	62
Diaphus fragilis	—	—	—	—	1	—	—	15	66	259	14	—	—	—	90	13	81	99	20	168	—	—	40	54
Triphoturus nigrescens	—	2	—	—	—	7	7	1	9	18	2	4	3	259	82	1,670	1,526	1,232	1,306	1,824	—	—	—	21
Ceratoscopelus warmingi	—	—	—	—	8	—	—	96	192	2,289	2	—	6	5,103	1,907	1,391	1,764	1,232	2,024	4,016	—	—	71	186
Myctophum nitidulum	6	2	12	4	1	13	3	10	11	3	2	—	3	2	1	2	1	—	24	20	—	—	—	—
Bolinichthys longipes	—	—	—	—	2	—	—	2	15	333	2	—	—	108	11	566	158	99	148	136	—	—	—	—
Diogenichthys laternatus	—	2	—	1,139	173	3	—	214	150	168	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gonichthys teniculus	2	4	4	1	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Diaphus garmani	—	—	—	114	63	—	—	1,085	359	485	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Diaphus problematicus	—	—	—	—	—	—	—	1	15	382	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lampanyctus nobilis	—	—	1	193	520	—	2	177	105	126	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lampanyctus omostigma	12	127	17	83	39	2	20	34	17	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Notoscopelus resplendens	—	—	—	9	26	—	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Diaphus malayanus	—	—	—	—	—	—	—	—	1	19	—	—	7	1,190	636	156	270	1,694	112	800	—	—	—	—
Diaphus regani	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	65	18	—	32	64	—	—	—	—
Diaphus signatus	—	—	—	—	—	—	—	—	—	—	—	—	—	112	97	604	2,025	2,299	4,400	3,804	—	—	—	—
Diaphus sp. (near *mollis*)	—	—	—	—	—	—	—	—	—	—	—	—	—	46	37	91	495	154	212	280	—	—	—	—
Lampanyctus hubbsi	—	—	—	—	—	—	1	1	1	1	—	—	1	259	43	175	45	33	44	—				
Myctophum asperum	—	—	—	—	—	2	13	13	26	77	3	3	7	1	16	3	43	253	236	26	—	—	2	3
Myctophum obtusirostrum	—	—	—	—	—	—	—	—	—	—	—	2	—	—	3	—	—	11	32	24	—	—	—	—
Diaphus elucens	—	—	—	—	—	—	—	—	—	—	34	—	—	39	32	—	—	—	—	—	—	—	—	—
Centrobranchus choerocephalus	—	—	—	—	—	—	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Total	1,524	472	308	1,785	960	599	845	2,403	1,631	5,356	181	237	279	7,515	3,197	6,408	7,319	8,358	10,722	12,866	100	146	392	516
Average, shallow or deep	768			1,372		722		3,130			232			5,356		9,134					123		454	

TABLE 4.—Species of myctophids and number taken per tow for stations given in Table 2.

Species	50 m		100 m		200 m		300 m		450 m		500 m	
Stn.	48	49	58	66	57	69	61	67	52	76	60	78
Electrona rissoi	—	—	—	—	—	—	—	1	—	—	—	—
Hygophum proximum	1	2	5	3	4	6	3	1	—	1	2	16
Diogenichthys atlanticus	3	3	4	—	—	1	1	—	—	1	—	5
Myctophum aurolaternatum	—	—	—	—	—	1	—	—	—	—	—	—
Myctophum asperum	3	—	—	1	—	—	—	—	—	—	—	—
Myctophum nitidulum	—	2	1	1	1	—	—	—	1	—	—	—
Myctophum obtusirostrum	1	—	—	1	—	—	2	—	—	—	1	—
Myctophum selenoides	—	—	3	—	—	—	1	—	—	—	—	—
Myctophum spinosum	—	2	2	—	1	1	1	—	—	—	—	—
Symbolophorus evermanni	5	8	9	8	3	—	1	2	—	1	—	1
Diaphus drachmani	—	—	—	—	—	—	1	—	—	1	—	—
Diaphus elucens	7	17	1	—	1	—	—	3	1	1	—	—
Diaphus fragilis	5	6	1	2	2	—	2	2	—	—	—	—
Diaphus jenseni	—	—	56	5	2	4	2	1	—	—	—	—
Diaphus longleyi	—	—	31	6	4	10	1	1	4	—	3	2
Diaphus lucidus	—	—	4	4	—	—	—	—	—	—	—	—
Diaphus luetkeni	2	—	4	—	3	4	1	—	2	2	2	1
Diaphus malayanus	67	10	1	2	1	1	—	2	—	—	—	—
Diaphus problematicus	—	—	2	—	—	—	—	—	—	—	—	—
Diaphus regani	—	—	1	—	—	—	—	—	—	—	—	—
Diaphus splendidus	7	—	46	14	6	2	5	3	—	2	5	1
Diaphus termophilus	—	—	—	1	—	7	3	3	6	1	—	1
Diaphus sp. (near *mollis*)	25	—	5	—	2	3	1	1	—	5	2	—
Notolychnus valdiviae	—	—	25	3	4	25	3	1	1	—	8	—
Lampadena luminosa	—	—	7	—	—	2	—	1	—	—	1	—
Triphoturus nigrescens	8	3	14	—	5	27	8	2	3	12	11	7
Lampanyctus hubbsi	78	66	7	4	4	8	—	2	1	4	—	2
Lampanyctus "niger"	—	—	43	23	34	127	13	31	42	11	1	28
Lampanyctus nobilis	—	—	—	—	—	—	1	—	—	1	—	—
Lampanyctus omostigma	—	—	—	—	—	—	—	—	—	1	—	—
Lampanyctus steinbecki	1	—	1	3	1	4	—	—	—	—	—	—
Bolinichthys sp.[1]	—	—	1	—	—	—	1	2	1	—	—	—
Bolinichthys longipes	12	10	1	2	2	1	1	—	3	1	—	1
Bolinichthys photothorax	—	—	2	—	—	—	2	2	1	—	—	—
Ceratoscopelus warmingi	90	123	25	2	10	12	11	14	1	8	5	3

[1]*Bolinichthys* sp. is similar to *B. supralateralis*, but is apparently distinct and undescribed (R. K. Johnson, Field Museum of Natural History, Chicago, Ill., pers. commun.).

Several of these species are truly warmwater cosmopolites (McGowan 1971). *Hygophum proximum*, *M. aurolaternatum*, *M. nitidulum*, and *B. longipes* occur in equatorial waters not only in the study area, but widely throughout the eastern equatorial Pacific. Others, *C. warmingi*, *Diogenichthys atlanticus*, and *Diaphus fragilis*, apparently occur in equatorial waters only west of ca. long. 130°W.

Most of the 10 above species showed similar trends in abundance with latitude; peak abundance was at either lat. 3°30′N or at the equator. The same trend is evident in the total numbers of myctophids taken in deep tows (Table 3). (The total catches of the shallow tows tended to decrease southward. This trend is not marked, and the absence of data from the equator is perhaps critical.) A trend similar to that of the deep catches and of the wide-ranging species has been noted in zooplankton standing crop (King and Hida 1957). The increases in abundance are probably related to the higher primary productivity resulting from the upwelling and subsequent northward transport of enriched waters near the equator (Cromwell 1953; Murphy and Shomura 1972).

Three species of myctophids which are abundant at night in the upper layers near Hawaii and also taken at the gyre center were conspicuously absent from the present samples. *Benthosema suborbitale*, *Diaphus schmidti*, and a *Diaphus* sp. similar to *D. mollis* (called *Diaphus* sp. A by Clarke 1973) are apparently restricted to the central water mass—at least to the east of long. 145°W.

Seven species occurred only or principally at the northern two stations. *Diogenichthys laternatus*, *Gonichthys teniculus*, *Diaphus garmani*, *Lampanyctus omostigma*, *L. nobilis*, and *Notoscopelus resplendens* were taken only at lat. 12°N and 7°30′N. *Diaphus problematicus* was taken only at lat. 7°30′N. Three of these species, *D. problematicus*, *L. omostigma*, and *L. nobilis*, were captured in the IK series at lat. 3°30′N, but in low numbers (Table 4). It is clear that none of these species occurred at lat. 3°30′N in abundance.

Of these seven species, one appears to be widely distributed in the central water masses and four

are widely distributed in the eastern equatorial Pacific. *Lampanyctus nobilis* is taken at the gyre center and consistently near Hawaii. Its distribution pattern at long. 145°W is thus intermediate between that of the three strictly central water-mass species mentioned above and that of the species which were taken all the way across the transect. *Diogenichthys laternatus, G. teniculus, L. omostigma,* and *N. resplendens* occur over a broad latitudinal range in the eastern equatorial Pacific and in a narrower tongue extending into the central equatorial Pacific (Wisner 1963, footnote 3; Bekker 1966). None of these species are taken near Hawaii, and only *G. teniculus* and *N. resplendens* are taken near the gyre center, neither very frequently.

Little is known of the distribution of *Diaphus garmani* and *D. problematicus* in the Pacific. *Diaphus garmani* has been reported from Johnson Island (Nakamura 1970). Wisner (footnote 3) reports it from near Hawaii but it was not taken there by Clarke (1973) nor does it occur at the gyre center. Ahlstrom (1972) recorded *D. garmani* in "an offshore equatorial belt" but mentions neither species as present in the eastern equatorial Pacific. In the Atlantic, both species occur in equatorial waters, but also occupy a broad latitudinal range in the west (Nafpaktitis 1968).

Five species were taken principally at lat. 3°30′N or the equator. *Diaphus signatus* and *D.* sp. (near *mollis* but apparently distinct from either of the *mollis*-like forms recorded from near Hawaii by Clarke) were taken in abundance at both stations, while *D. regani* was taken almost exclusively at the equator. A few *D. malayanus* and *Lampanyctus hubbsi* were taken at lat. 7°30′N, but these species were clearly more common at lat. 3°30′N and the equator. All of these species are found only in the Pacific. There are no reports of any from either the eastern equatorial Pacific or the eastern section of the central water mass. *Lampanyctus hubbsi* is restricted to the offshore equatorial water mass (Wisner 1963). The same is apparently true of the undescribed species of *Diaphus* (Wisner footnote 3). The other three species of *Diaphus* were originally described from farther south or west and near island groups (Gilbert 1908; Weber 1913; Tåning 1932), and a few were collected in the western Pacific by Kulikova (1961). Wisner (footnote 3) indicates that they occur, like *L. hubbsi,* in the narrow offshore equatorial region between ca. long. 130-170°W.

Diaphus elucens was taken only at lat. 3°30′N, and *Myctophum obtusirostrum* at lat. 3°30′N and the equator. Their distributions are however, much broader than the present data indicates (Nafpaktitis 1968, 1973). Both are taken consistently near Hawaii. It seems likely that their capture only at the above latitudes was due more to their greater abundance there as opposed to their absence from the other latitudes sampled. *Centrobranchus choerocephalus* was taken only twice (lat. 7°30′N and 3°30′N). Bekker (1966) suggests it is a central water-mass species, and it is taken regularly near Hawaii. No real significance can be attached to the capture of only two specimens in the equatorial water mass.

The remaining species, *Myctophum asperum,* was taken at all latitudes except lat. 12°N. Its distribution in the Pacific is poorly known. Ahlstrom (1972) records it from lat. 7°N to 2°S between long. 98° and 119°W. It is not taken at the gyre center or near Hawaii. It is apparently, like *Diaphus garmani* and *D. problematicus,* neither a central nor eastern equatorial species, but may have a broader distribution to the west.

Although the data from both the present study and the literature are admittedly fragmentary and we know nearly nothing about distributions south and west of the study area, the evidence indicates that there is no distinct or abrupt change between the shallow-water myctophid faunas of the central and equatorial water masses as defined by Sverdrup et al (1942). While there are at least three abundant central species which did not occur in our equatorial samples, there were more which occurred throughout the sampling area and, in most cases, are also widely distributed in equatorial waters farther east. In between are several central species which occur in the equatorial water mass to a limited extent—both latitudinally (*L. nobilis*) and longitudinally (*Ceratoscopelus warmingi, Diogenichthys atlanticus,* and *Diaphus fragilis*).

Within the equatorial water mass, however, there is a distinct and rather abrupt change in fauna. Four species which occur throughout equatorial waters farther east were taken only at the northern two stations, while five other species which do not occur east of ca. long. 120-130°W were taken at lat. 3°30′N and the equator. There is thus little or no overlap between the ranges of the strictly offshore and those of the eastern equatorial species whose ranges extend into the study area.

The change in fauna is close to the northern

boundary of the SEC and may be related to the upwelling and northward transport of surface waters near the equator. In Figure 1, the latter are indicated by the shallow 27°C isotherm between about lat. 1°S and 0°30'N—somewhat south of the indicated faunal change. However, King and Hida (1957) and Murphy and Shomura (1972) point out that, while strength of upwelling and extent of northward surface transport vary irregularly over short periods depending on strength and direction of winds, the area between about lat. 1°S and about lat. 4°N can be regarded as a zone of high primary production and high zooplankton standing crop over most of the year.

The central equatorial Pacific is thus somewhat unique in that it is the only major offshore and truly oceanic area in the world where upwelling and high primary production are not strongly seasonal. Other areas of upwelling are either relatively close to land or, e.g., the Antarctic, are light-limited over part of the year. Thus it is not surprising that the fauna of the zone is different from both that of the oceanic, but relative sterile central water mass and that of the highly productive, but less oceanic eastern equatorial Pacific. Nor is it surprising that five of the species which occur in the zone are either endemic or restricted to it at least in the eastern part of the Pacific.

The faunal change observed in the data here could in part be a consequence of the change in primary production and availability of food. Ebeling (1962) has suggested that distributions of even deep-living, nonmigrating fishes are associated with differences in surface primary production, and Backus et al. (1969) have suggested that faunal changes associated with thermal fronts are more directly related to differences in primary production which result from differences in thermal structure on either side of the front. It is not unreasonable to suggest that the five species which were found only near the equator are unable to survive in the less productive waters north of about lat. 4°N.

This is, of course, insufficient to explain other features of the faunal change. It is not clear why some species, many which occur also in sterile central waters, not only occur in the equatorial zone of high production but are markedly more abundant there, while other species, which occur in the highly productive eastern equatorial Pacific, are apparently excluded from the offshore zone near the equator. More knowledge, e.g., the reproductive potential and food requirements, of the species concerned and of environmental characteristics of the areas, e.g., types and rates of predation, is needed before even speculation is warranted.

There are several examples where dominant species are "replaced" by congeners or morphologically similar species. *Lampanyctus omostigma* and *L. hubbsi* are very similar congeners which both occur in the equatorial water mass but with separate distributions. *Diaphus schmidti*, a central water-mass species, is replaced by *D. garmani* and *D. problematicus* in the northern section of the equatorial water mass, and these in turn are replaced by *D. malayanus*, *D. signatus*, and *D. regani* in the zone near the equator. All these *Diaphus* species are similar morphologically. *Diaphus schmidti*, *D. garmani*, and *D. malayanus* are of similar size at maturity while the others are somewhat larger. In addition to differences in placement of body photophores and development of sexually dimorphic head organs, these species are all distinguished by slightly different gill raker counts, suggesting differences in feeding habits. The *Diaphus mollis*-like forms also show a replacement series of sorts. The central water-mass species (*Diaphus* sp. A of Clarke 1973) is very similar in size and morphology to the *Diaphus* sp. taken near the equator; however, no similar form was present in the northern section of the equatorial water mass.

It is not implausible to suggest that *Benthosema suborbitale* and the *Diogenichthys* species form a replacement series. *Benthosema suborbitale* is a diminutive species of *Benthosema* and very similar to the *Diogenichthys*; the two genera are closely related (Moser and Ahlstrom 1970; Paxton 1972). It is apparently replaced by *D. laternatus* in the northern section of the equatorial water mass. *Diogenichthys atlanticus* occurs in all three zones, but is an abundant and dominant species only near the equator—where neither *B. suborbitale* nor *D. laternatus* occur.

Clarke (1973) has shown that, at a single location, closely related species have different nighttime depth ranges. The data here suggest that within a given depth range, closely related species are frequently separated geographically. Investigations of the biology of such closely related, but separated species, particularly near their geographic boundaries, would be a promising approach toward understanding the factors determining zoogeographic distribution in the open ocean.

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LITERATURE CITED

AHLSTROM, E. H.
1971. Kinds and abundance of fish larvae in the eastern tropical Pacific, based on collections made on EASTROPAC I. Fish. Bull., U.S. 69:3-77.
1972. Kinds and abundance of fish larvae in the eastern tropical Pacific on the second multivessel EASTROPAC survey, and observations on the annual cycle of larval abundance. Fish. Bull., U.S. 70:1153-1242.

BACKUS, R. H., J. E. CRADDOCK, R. L. HAEDRICH, AND D. L. SHORES.
1969. Mesopelagic fishes and thermal fronts in the western Sargasso Sea. Mar. Biol. (Berl.) 3:87-106.

BEKKER, V. E.
1965. Lanternfishes of the genus *Hygophum* (Myctophidae, Pisces), systematics and distribution. Akad. Nauk SSSR, Tr. Inst. Okeanol. 80:62-103. (Transl. 45, Natl. Mar. Fish. Serv., Syst. Cent., U.S. Natl. Mus.)
1966. Slendertailed luminescent anchovies (genera *Loweina, Tarletonbeania, Gonichthys* and *Centrobranchus*) of the Pacific and Indian Oceans. Systematics and distribution. *In* T. S. Rass (editor), Fishes of the Pacific and Indian Oceans biology and distribution, p. 10-78. (Translated from Russ. by Israel Program Sci. Transl., available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va, as TT 65-50120.) (Original 1964 in Akad. Nauk SSSR, Tr. Inst. Okeanol. 73:1-75.)

CLARKE, T. A.
1973. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. Fish. Bull., U.S. 71:401-434.

CROMWELL, T.
1951. Mid-Pacific oceanography, January through March, 1950. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 54, 76 p.
1953. Circulation in a meridional plane in the central equatorial Pacific. J. Mar. Res. 12:196-213.

EBELING, A. W.
1962. Melamphaidae I. Systematics and zoogeography of the species in the bathypelagic fish genus *Melamphaes* Günther. Dana Rep., Carlsberg Found. 58, 164 p.

FAGER, E. W., AND J. A. MCGOWAN.
1963. Zooplankton species groups in the North Pacific-. Science (Wash., D.C.) 140:453-460.

GIBBS, R. H., JR., R. H. GOODYEAR, M. J. KEENE, AND D. W. BROWN.
1971. Biological studies of the Bermuda Ocean Acre. II. Vertical distribution and ecology of the lanternfishes (family Myctophidae). Rep. to U.S. Navy Underwater Syst. Cent., Smithsonian Inst., Wash., 141 p.

GILBERT, C. H.
1908. Reports on the scientific results of the expedition to the tropical Pacific, in charge of Alexander Agassiz on the U.S. Fish Commission steamer "Albatross" from August, 1899, to March 1900, Commander Jefferson T. Moser, U.S.N., commanding. X. The lantern fishes. Mem. Mus. Comp. Zool., Harvard Univ. 26(6):217-237.

GRANDPERRIN, R., AND J. RIVATON.
1966. "Coriolis": Croisière "Alizé" Individualisation de plusieurs ichtyofaunes le long de l'équateur. [In Fr., Engl. summ.] Cah. O.R.S.T.O.M. (Off. Rech. Sci. Tech. Outre-Mer), Sér. Oceanogr., 4(4):35-49.

HIGGINS, B. E.
1970. Juvenile tunas collected by midwater trawling in Hawaiian waters, July–September 1967. Trans. Am. Fish. Soc. 99:60-69.

JOHNSON, M. W., AND E. BRINTON.
1963. Biological species, water-masses and currents. *In* M. N. Hill (editor), The sea. Ideas and observations on progress in the study of the seas. Vol. 2. The composition of sea-water, comparative and descriptive oceanography, p. 381-414. Interscience Publ., N.Y.

KING, J. E., AND T. S. HIDA.
1957. Zooplankton abundance in the central Pacific, Part II. U.S. Fish. Wildl. Serv., Fish. Bull. 57:365-395.

KOBLENTZ-MISHKE, O. J., V. V. VOLKOVINSKY, AND J. G. KABANOVA.
1970. Plankton primary production of the world ocean. *In* W. S. Wooster (editor), Scientific exploration of the South Pacific, p. 183-193. Natl. Acad. Sci., Wash., D.C.

KULIKOVA, E. B.
1961. Data on the lantern fishes of the genus *Diaphus* (family Scopelidae) from the western part of the Pacific Ocean. Akad. Nauk SSSR, Tr. Inst. Okeanol. 43:5-39. (Transl. 61, 42 p., Natl. Mar. Fish. Serv., Syst. Cent., U.S. Natl. Mus.)

MCGOWAN, J. A.
1971. Oceanic biogeography of the Pacific. *In* B. M. Funnell and W. R. Riedel (editors), The micropaleontology of oceans, p. 3-74. Cambridge Univ. Press, Cambridge, Engl.

MOSER, H. G., AND E. H. AHLSTROM.
1970. Development of lanternfishes (family Myctophidae) in the California Current. Part I. Species with narrow-eyed larvae. Bull. Los Ang. Cty. Mus. Nat. Hist. Sci. 7, 145 p.

MURPHY, G. I., AND R. S. SHOMURA.
1972. Pre-exploitation abundance of tunas in the equatorial central Pacific. Fish Bull., U.S. 70:875-913.

NAFFAKTITIS, B. G.
1968. Taxonomy and distribution of the lanternfishes, genera *Lobianchia* and *Diaphus*, in the North Atlantic. Dana Rep., Carlsberg Found. 73, 131 p.
1973. A review of the lanternfishes (Family Myctophidae) described by Å. Vedel Tåning. Dana Rep., Carlsberg Found. 83, 46 p.

NAFFAKTITIS, B. G., AND M. NAFFAKTITIS.
1969. Lanternfishes (family Myctophidae) collected during

cruises 3 and 6 of the R/V *Anton Bruun* in the Indian Ocean. Bull. Los Ang. Cty. Mus. Nat. Hist. Sci. 5, 79 p.

NAKAMURA, E. L.
1970. Observations on the biology of the myctophid, *Diaphus garmani*. Copeia 1970:374-377.

PAXTON, J. R.
1972. Osteology and relations of the lanternfishes (family Myctophidae). Bull. Los Ang. Cty. Mus. Nat. Hist. Sci. 13, 81 p.

SVERDRUP, H. U., M. W. JOHNSON, AND R. H. FLEMING.
1942. The oceans. Their physics, chemistry, and general biology. Prentice-Hall, Inc., Englewood Cliffs, N.J., 1087 p.

TÅNING, A. V.
1932. Notes on scopelids from the Dana Expeditions. Vidensk. Medd. Dan. Naturhist. Foren. Kbh. 94:125-146.

WEBER, M.
1913. Die fische der Siboga-expedition. Siboga-expeditie 65:1-710.

WISNER, R. L.
1963. *Lampanyctus hubbsi*, a new myctophid fish from the East-Central Tropical Pacific Ocean, with notes on the related, sympatric Eastern Pacific species, *L. omostigma* and *L. parvicauda*. Copeia 1963:16-23.

YEAR-TO-YEAR VARIATIONS IN THE PLANKTOLOGY OF THE OREGON UPWELLING ZONE

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ABSTRACT

Sampling results from Oregon coastal waters show that plankton abundance in 1971, a year of reduced coastal upwelling, was lower than in 1969 or 1970. This was correlated with greater frequency and abundance in 1971 for species usually found more offshore and with a general reduction in the number and density of the most strictly neritic species. It is proposed that these changes are related to changes in nearshore fisheries which, therefore, appear to depend upon the general stimulation of production by upwelling.

In this paper we describe the nearshore zooplankton community found off the Oregon coast during the upwelling seasons of 1969, 1970, and 1971. Differences in species composition and abundance between the individual upwelling seasons will be described and related to differences in upwelling strength, hydrographic conditions, and wind patterns. Our research on coastal zooplankton is centered upon understanding the dynamics of the nearshore community found within 18 km of the beach. We have concentrated our efforts in this area because it has been shown to be the location of the most intense coastal upwelling. Effects of upwelling are present farther offshore, but the phenomenon is most pronounced within 10 km of shore (Huyer 1974). The importance of understanding coastal upwelling and its effect upon biological production is well established.

PREVIOUS ZOOPLANKTON STUDIES IN THE OREGON AREA

Distribution and abundance of Oregon coastal zooplankton has been the subject of several theses at Oregon State University. Seasonal variations in distribution and abundance along a single line of latitude have been studied by Hebard (1966) off Newport (Figure 1) and by Laurs (1967) off Brookings. Both seasonal and spatial variations were considered by Cross (1964) from data collected off Astoria, Newport, Coos Bay, and Brookings. Lee (1971) looked at samples collected from a grid of stations during one brief interval in August 1963. Both Hebard and Laurs employed plankton nets with a mesh size of 570 μm while Cross and Lee used nets with 240-μm mesh. Since the larger mesh retained only very large forms, some very different conclusions about the relative importance of zooplankton species were reached by the different authors. Hebard found that the euphausiid *Euphausia pacifica* was numerically dominant, and Laurs found that this animal dominated the zooplankton biomass. Copepods were unimportant in their studies. Conversely, Cross and Lee found that the copepods *Oithona similis*, *Pseudocalanus*, and *Acartia longiremis* were numerically dominant. A forthcoming paper by Pearcy (in litt.) will summarize the results of a

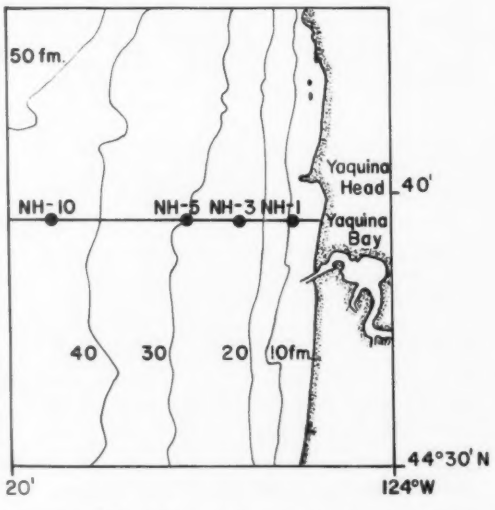

FIGURE 1.—Map of the study area showing the Newport hydrographic line (solid dark line) and the sampling positions.

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4-yr study of seasonal biomass cycles at distances of 28 km from shore and beyond, which employed mid-water trawls and 570-μm plankton nets.

Peterson (1972) summarized the results of 434 zooplankton samples collected off Oregon and Washington with 110-μm mesh Clarke-Bumpus nets at an irregular set of stations in 1961 and 1962. Most of the samples were taken beyond the continental shelf break. His conclusion that copepods attain larger inshore populations in winter than in summer is not in agreement with our results for the Oregon nearshore zone. We have found winter densities to be several orders of magnitude lower than summer densities. This discrepancy makes his work difficult to evaluate.

All of these studies share two shortcomings: First, few or no samples were collected within 10 km of the coast. Second, the time intervals between samplings were large, ranging from monthly (Hebard 1966) to quarterly and longer (Cross 1964; Laurs 1967; Peterson 1972). Under such sampling programs the authors could only document large scale phenomena, such as faunal changes associated with seasonal hydrographic changes, and faunal differences between nearshore and offshore stations.

THE COASTAL ENVIRONMENT OF OREGON

Aspects of descriptive physical oceanography of Oregon coastal waters can be found in Burt and Wyatt 1964; Pattullo and Denner 1965; Cross and Small 1967; Collins et al. 1968; Bourke 1972; Pillsbury 1972; Huyer 1974; and Smith 1974.

Circulation Patterns

The California Current is a slow, southward-flowing current situated within a band 300 to 800 km off the Oregon coast. Inshore of this permanent feature the circulation changes with season. During spring and summer months nearshore flow is southward, driven by northerly winds. During fall and winter months, after cessation of upwelling, flow is northward. This flow is called the Davidson Current.

Wind and Coastal Upwelling

Northerly winds predominate from April to September. They produce a generally southward transport of surface water with a component to the right of the wind away from the coastline. This offshore, near-surface transport is balanced by northward and onshore transport at depth of cool, high salinity, nutrient rich water. When northerly winds are strong and/or persistent, cold, high salinity water appears on the beach and throughout the entire water column out to about 10 km. This condition is called active or intense upwelling. When north wind stress is weak or nonexistent, this onshore deep transport is weakened and nearshore waters are warmed by solar radiation.

Intense upwelling is not a continuous process during summer, but occurs sporadically. If northerly winds blow for a day or two, upwelling will develop. If wind ceases or changes direction, upwelling ceases. During July and August northerly winds are often persistent, so that intense upwelling may continue for several weeks without interruption.

Waters offshore of 10-20 km do not experience these rapid changes. In these deeper waters, upwelling is indicated in hydrographic sections by upward sloping isolines of temperature, salinity, and density (see Smith 1974). The upward slope develops in April or May and persists until cessation of upwelling in September or October. Offshore surface waters are warm (as high as 17°C) and a mixed layer is well developed. Salinities are reduced as a result of the Columbia River plume.

Temperature and Salinity Relationships

Pillsbury (1972) has summarized all temperature and salinity data collected within the top 10 m of the water column at stations 5 and 9 km from shore during the April-September upwelling seasons of 1960 through 1970, a total of 188 observations. Pillsbury used the modal cell technique of Pattullo and Denner (1965) to summarize the data. The portion of a temperature-salinity plot containing the most data points was one bounded by 8.1°-9.0°C and 33.1-34.0‰. That "cell" accounted for 28% of the data. Pillsbury identified two general water types that occur at the two stations: 1) cold-upwelled water (7.5°-8.5°C and 33.5-34‰) and 2) warm, low salinity water (11.0°-12.0°C and 30.5-31.5 ‰) which is a mixture of Columbia River plume water and surface oceanic water.

MATERIALS AND METHODS

Zooplankton were collected along the Newport Hydrographic (NH) line, lat. 44°40'N. We chose this line because extensive hydrographic data are available from cruises made since 1960. Station labels NH 1, NH 3, NH 5, and NH 10 refer to distances in nautical miles from shore and are approximately 2, 5, 9, and 18 km from the beach. Figure 1 is a map of the study area.

Zooplankton samples were collected with 20-cm "Bongo" nets without an opening-closing mechanism. To construct the net frame, two 20-cm diameter × 30-cm PVC (polyvinyl chloride) cylinders were bolted to either side of a pivoting wire clamp. When mounted on the towing cable the net frame was free to move in the vertical plane about 120° of arc, and it could rotate horizontally about the towing cable.

The two plankton nets were 145 cm long and were constructed of NITEX[2] nylon with mesh aperatures of 505 and 240 μm. The ratio of net mesh area to net mouth area was about 11.5:1 for the 240-μm net. The cod ends were 9-cm diameter × 16-cm PVC buckets with stainless steel mesh screens cemented to laterally positioned filtering windows. The two cod ends were fastened about 15 cm apart with a stainless steel strap which kept the nets from wrapping about the cable while being towed. Tsurumi-Seiki Kosakusho flowmeters were mounted off-center in each net mouth. Tows were made obliquely over the entire water column using either a V-fin or Kite-Otter depressor. A time-depth recorder was used to record the towing track. Samples were preserved with 10% buffered formaldehyde solution.

In the laboratory, samples were poured into 500-ml pharmaceutical graduates and allowed to settle. Several hours later the settled volume was read. Water was then decanted off or added to make a diluted volume of five times the settled volume. Aliquots for counting were removed from this volume with a 1-ml Stempel pipette, after the animals were suspended by agitation with a small spatula.

Animals were enumerated with the aid of a binocular dissecting microscope at 25× magnification. Five aliquots were drawn from each sample. Taxa were counted in the first and successive aliquots until 50 in a category were enumerated. These counts were multiplied by appropriate factors to arrive at a number of individuals in a category per five aliquots. A computer was used to convert these raw data into number of individuals per cubic meter and to carry out much of the summary data analysis.

All adult copepods were divided by sex and identified to species. Two morphs of the genus *Metridia* were seen and were separated on the basis of shape of the prosome in lateral view. The *Metridia pacifica* type is more robust and has a steeply sloping forehead, while the *M. lucens* type has a much less sloping forehead. Detailed morphological study of the two types has not been done. Copepodite stages were identified for all species except those of *Clausocalanus*. Only the nauplii of *Calanus* sp. were distinguished. Both euphausiids and cladocerans were identified to species. All other holoplanktonic taxa were grouped (e.g., amphipods, ostracods, medusae, ctenophores, chaetognaths, etc.). Meroplankton were counted as general categories: barnacle nauplii, crab zoea, bivalve veligers, etc. The crab larvae were not counted because they are being studied by R. Gregory Lough, School of Oceanography, Oregon State University.

Surface temperature was measured at all stations and a surface salinity sample was gathered at nearly all stations. Bottom salinity samples were taken on many cruises. Bathythermograph traces were taken at most stations.

Hourly wind data were supplied by William Gilbert, School of Oceanography, Oregon State University. They were gathered by the National Weather Service, NOAA (National Oceanic and Atmospheric Administration) from a recording anemometer located on the south jetty off Newport, Ore., and are stored on magnetic tapes as north-south and east-west components. We determined the resultant vector from the daily mean components and constructed progressive vector diagrams (PVD's) for each upwelling season.

RESULTS

Hydrography and Wind Data

We have compared our surface temperature and salinity data to Pillsbury's modal cell. Data collected during the upwelling seasons 1969-71, from NH 1, NH 3, and NH 5 are shown in Figure 2. None of our observations were part of Pillsbury's data. Striking differences between upwelling

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

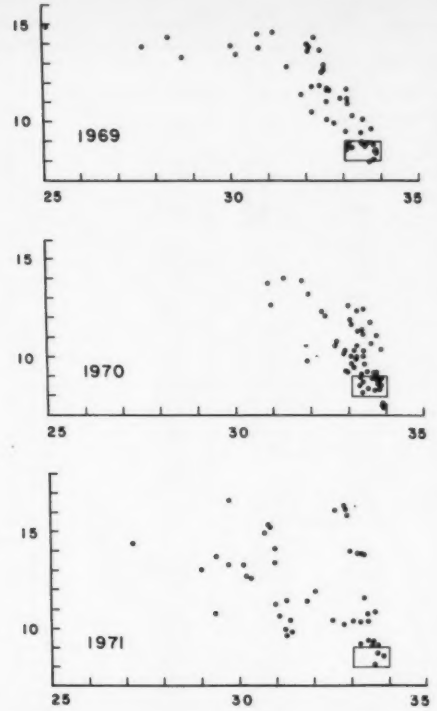


FIGURE 2.–Temperature-salinity diagrams for NH 1, NH 3, and NH 5 in 1969, 1970, and 1971 between April and September.

seasons are seen. About 26% of the 1969 and 1970 data fell within the limits of the modal cell (8.1°-9.0°C and 33.1-34.0 ‰). Only 6% of the 1971 data fell within the limits. Water was generally warmer and of a lower salinity during most of the 1971 upwelling season. Higher temperatures and lower salinities indicate the presence of mixed Columbia River plume water and surface oceanic water. Both the modal cell and surface temperature observations indicate that upwelling was weaker in 1971 than in 1969 or 1970.

Wind data supports the conclusion that the upwelling season of 1971 was a weak one. The PVD's (Figure 3) illustrate the pattern of the wind from 1 May through 30 September for the years 1969-71. They give an indication of amounts of upwelling-inducing northerly winds during a given season, and are useful for comparing different seasons. The axes of the PVD's are wind-miles (i.e., miles per hour multiplied by hours). The northerly component of the wind extends positively down the ordinate and westerly component extends positively along the abscissa. The seasonal pattern for 1971 is quite different from 1969 and 1970. Northerly wind miles are low while westerly wind miles are exceptionally high. Therefore, upwelling should have been relatively weak. This explains the low frequency of temperature and salinity observations in the modal cell in 1971, compared to 1969 or 1970. The 1969 and 1970 wind patterns are similar; 1969 had about 2½ mo of persistent northerlies, while 1970 had about 4 mo of persistent northerlies. A higher total northerly component was achieved in 1970 than in 1969.

The upwelling index data of Bakun (1973) show 1969 and 1970 to have been close to average years compared with the years 1946 to 1971, while 1971 was far below average. These monthly indices estimate the magnitude of the offshore component of the Ekman transport and are calculated from an estimate of the mean monthly sea surface wind stress, which is based in turn on a geostrophic wind calculation from pressure field data. The anomalies of the index at lat. 45°N, long. 125°W for the periods of interest in our study are:

Month	*25 yr mean index for month*	*1969*	*1970*	*1971*
May	34	-22	- 1	+32
June	48	+13	- 2	-36
July	74	+32	- 3	- 9
Aug.	51	- 5	+23	-27
Sept.	17	-11	- 5	- 8
Total		+ 7	+12	-48

Bakun's indices were derived from different data than the PVD's and comparisons between years would not be expected to be in exact agreement.

Total Zooplankton

Table 1 is a list of the sampling dates and total zooplankton abundance at stations NH 1, 3, 5, and 10. The 1972 data set is shown, but since so few samples were taken relative to the number gathered in other years, we have eliminated these data from comparative discussions. One can see several patterns in Table 1. Abundances are usually highest at the station nearest the shore (2 km from the beach). Abundances grade to lows at the station 18 km from shore. They continue to decrease farther from shore (Cross 1964). There is

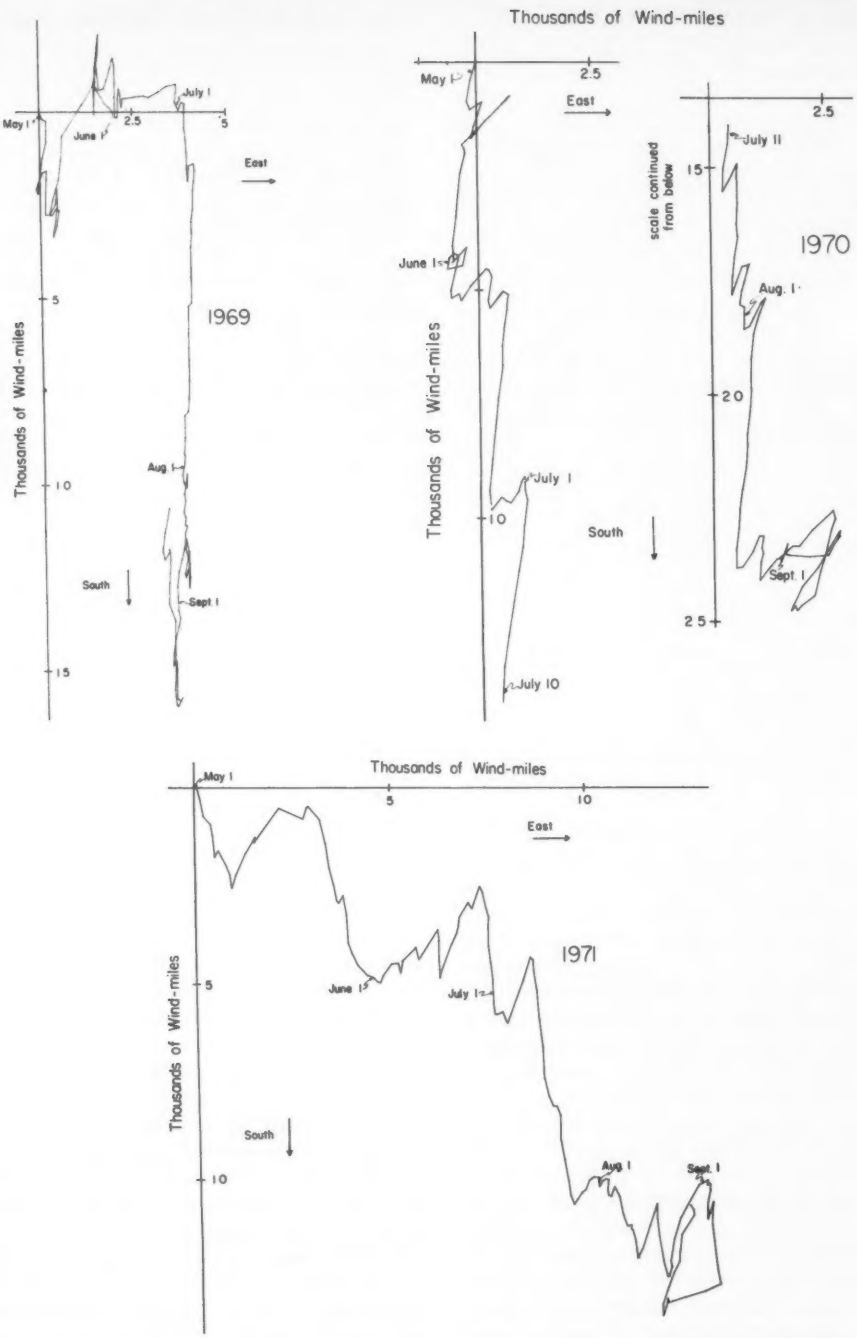


FIGURE 3.—Progressive vector diagrams for the wind at the Newport jetty between May 1 and September 30 in 1969, 1970, and 1971.

TABLE 1.–A list of sampling dates and total zooplankton catch (individuals/m³) at stations NH 1, 3, 5, and 10. These stations are approximately 2, 5, 9, and 18 km from shore.

Date	NH 1	NH 3	NH 5	NH 10
1969:				
22 June	15,305	2,780	2,375	553
29 June	—	3,712	—	3,895
10 July	15,097	—	8,016	—
18 July	44,782	3,442	10,131	766
25 July	16,277	30,633	1,042	1,334
6 Aug.	9,531	7,482	2,940	—
26 Aug.	—	—	1,721	90
30 Aug.	9,069	6,150	3,141	998
3 Sept.	4,344	3,051	4,756	3,058
14 Sept.	—	5,707	4,447	—
28 Sept.	—	3,457	3,368	—
1970:				
27 Apr.	105	606	767	797
6 May	1,393	872	—	158
22 May	1,166	1,793	1,739	178
4 June	5,375	614	1,185	—
23 June	51,372	1,118	59	434
2 July	30,952	3,633	3,172	2,136
16 July	6,495	4,195	1,935	1,508
29 July	—	4,198	3,179	1,833
13 Aug.	4,135	—	2,202	108
23 Aug.	5,846	4,070	1,264	1,846
11 Sept.	3,121	9,307	322	2,406
25 Sept.	11,450	5,806	6,263	4,349
1971:				
3 May	1,153	1,820	933	927
14 May	967	1,660	1,292	1,679
29 May	4,691	741	1,410	1,715
2 June	—	2,721	—	—
12 July	8,276	4,075	2,086	2,385
28 July	6,737	973	765	—
6 July	3,638	313	674	1,482
21 July	9,577	1,236	1,069	760
2 Aug.	4,276	1,370	2,940	886
19 Aug.	1,559	1,165	531	388
23 Sept.	1,023	896	565	613
1972:				
20 Apr.	1,123	—	1,131	1,057
22 May	2,553	1,652	164	194
11 June	1,242	952	2,578	913
28 June	3,108	1,293	1,090	1,606
21 July	1,372	886	1,071	1,835
5 Aug.	2,589	—	338	575

a seasonal pattern in total zooplankton abundance. Low abundances always occur in April, May, and early June. Low abundances occur at various times during summer and fall as well. Peak abundances occurred in late June and July during 1969 and 1970. No such peak developed in 1971. As a result, standing stocks in 1971 were much lower than other years. There is some indication that 1972 may have had low standing stocks as well.

Table 2 shows the average catch at each station for three seasons. The 1969 data are biased since there are no samples for spring months. To make the average catch data comparable, samples averaged for 1970 began with 23 June and for 1971 began with 12 June. As with temperature-salinity and wind data, 1971 is markedly different from 1969 and 1970, particularly close to shore. This inference was tested by the Kruskal-Wallis sum of ranks test. Medians for the 3 yr were found to be significantly ($P < 0.05$) nonhomogeneous at all of the stations except NH 10.

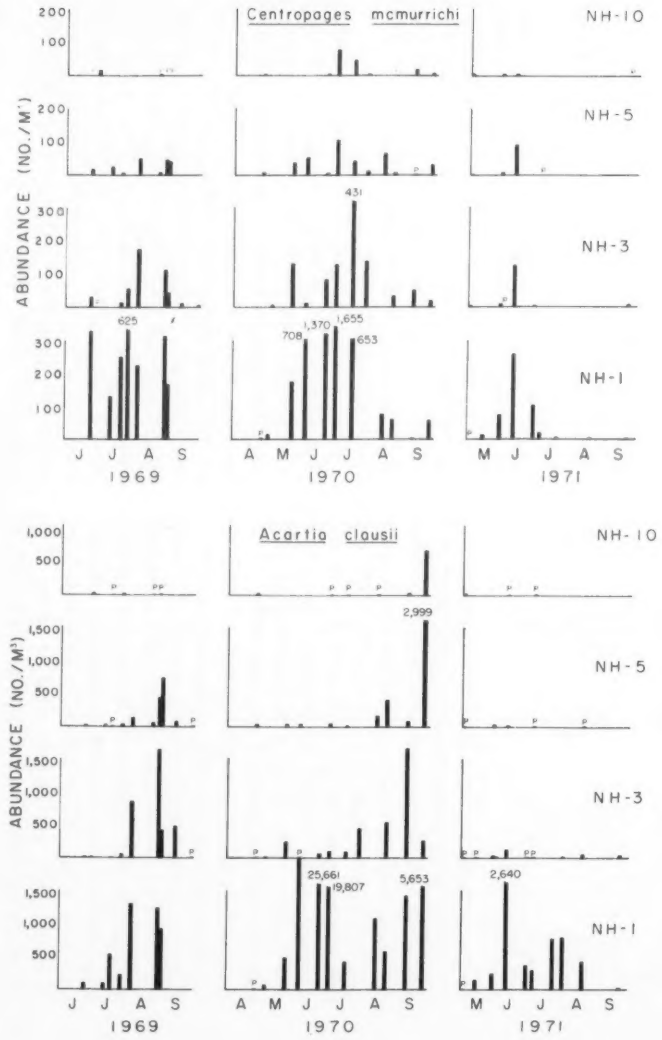
TABLE 2.–Average catch of zooplankton at stations NH 1, 3, 5, and 10 for each upwelling season. Not all sampling dates are included in the mean because the 1969 data are biased since the first samples were collected on 22 June. Therefore, to make all data sets comparable, only samples taken from 23 June through September 1970 and 12 June through September 1971 were used.

Year	NH 1	NH 3	NH 5	NH 10
1969	16,344	7,379	4,090	1,528
1970	16,196	4,618	2,300	1,828
1971	5,012	1,433	1,233	1,066

Zooplankton Species

Copepods are the dominant zooplankters in our samples. In 100 of 137 samples collected 1969-72, they account for more than 90% of the total catch. In the remaining samples they made up at least 50%. Several species of copepods were individually dominant or shared dominance: *Calanus marshallae* Frost (1974), *Pseudocalanus* sp., *Centropages abdominalis* Sato (= *C. mcmurrichi* Willey), *Acartia clausii* Giesbrecht, *A. longiremis* Lilljeborg, and *Oithona similis* Claus. These copepods are responsible for the patterns of seasonal and spatial abundance seen in Table 1. Individual species patterns are illustrated in Figures 4 and 5. *Pseudocalanus* sp., *A. clausii*, and *C. abdominalis* are grouped in Figure 4 because they are most abundant at the station nearest the beach. Figure 5 contains *A. longiremis* and *Calanus* sp. because they are usually more abundant farther offshore. *Oithona similis* abundance has no certain relationship to distance offshore within 18 km of the coast. Other species exhibit similar abundance gradients but they will not be discussed in this paper.

Table 3 lists relative density and frequency of occurrence of all copepod species. Relative density is the average number of individuals in samples in which the species occurred. The values in the table are sums of relative densities at the four stations for individual years. Table 4 lists relative density and frequency of occurrence of other holoplanktonic taxa and of the meroplankton. The taxa that occurred most frequently or were abundant include chaetognaths (*Sagitta elegans* Verrill predominantly), bivalve veligers, barnacle nauplii, euphausiid eggs, and small round eggs which are probably *Calanus* eggs.



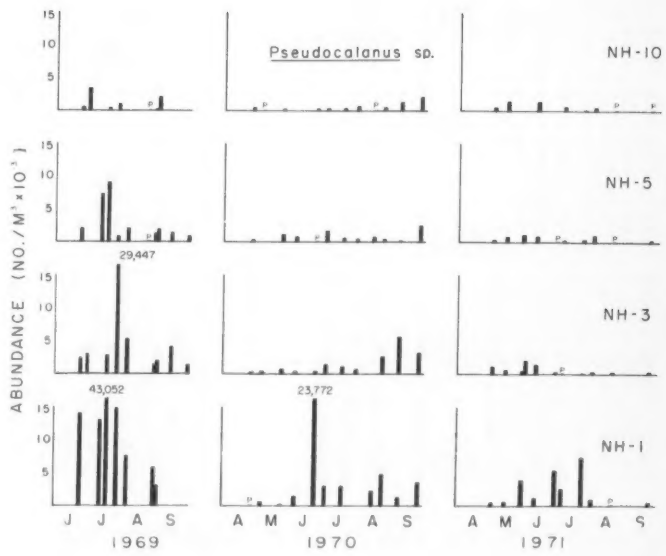
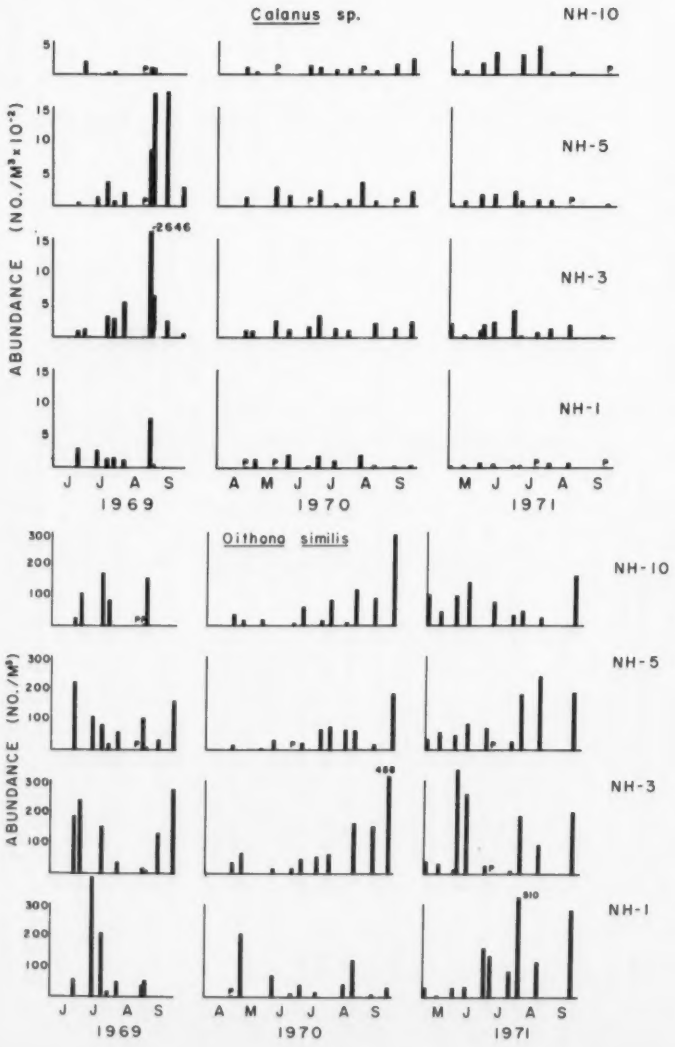


FIGURE 4.—Density of *Pseudocalanus* sp., *Acartia clausii*, and *Centropages mcmurrichi* (= *C. abdominalis*) at NH 1, NH 3, NH 5, and NH 10 in the upwelling seasons of 1969, 1970, and 1971.



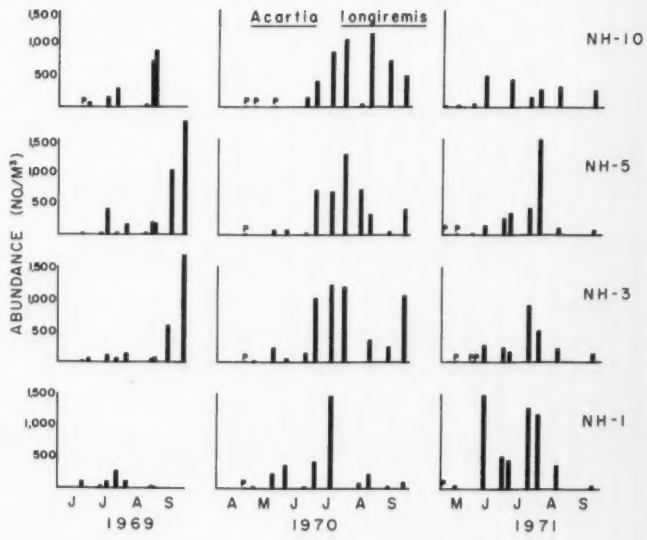


FIGURE 5.—Density of *Calanus* sp., *Acartia longiremis*, and *Oithona similis* at NH 1, NH 3, NH 5, and NH 10 in the upwelling seasons 1969, 1970, and 1971.

TABLE 3.–Total relative density and frequency of occurrence of the copepod species taken within 18 km of the Oregon coast, during 1969, 1970, and 1971. Relative density is average number of individuals per cubic meter in samples in which the species occurred. The table entries represent the sums of relative density at each of four stations. A total of 33 samples were collected in 1969, 44 in 1970, and 40 in 1971.

	Total relative density			Frequency		
Species[1]	1969	1970	1971	1969	1970	1971
Calanus sp.	1,475.2	482.5	436.1	32	44	40
C. tenuicornis	1.3	5.1	7.9	1	4	14
Eucalanus bungii	21.1	3.1	9.0	13	10	15
Paracalanus parvus	80.7	147.3	16.8	29	21	20
Pseudocalanus sp.	23,776.3	6,682.4	3,994.5	33	44	40
Microcalanus pusillus	2.2	18.5	1.8	4	17	2
Clausocalanus arcuicornis	0	1.4	4.0	0	3	7
C. pergens	20.2	5.9	6.6	5	5	9
Clausocalanus immatures	0	0.5	2.1	0	5	2
Ctenocalanus vanus	4.8	31.0	11.0	5	7	16
Aetideus pacificus	1.5	2.3	2.7	4	4	1
Gaidius immatures	2.5	3.4	3.7	3	3	2
Racovitzanus antarcticas	0.6	2.1	1.3	1	2	2
Scolecithricella minor	9.3	4.6	16.0	7	14	16
Metridia lucens	21.4	16.3	48.6	18	29	26
M. pacifica	6.7	2.9	3.7	2	5	6
Lucicutia flavicornis	0	0.4	2.0	0	1	9
Centropages abdominalis	371.8	686.2	110.7	29	42	23
Epilabidocera longipedata	2.9	10.8	0	5	6	0
Acartia clausii	1,178.1	6,045.1	414.9	31	37	29
A. longiremis	1,078.2	1,509.2	1,331.1	33	44	38
A. tonsa	130.7	27.5	0	31	19	0
Tortanus discaudatus	17.5	12.3	0	3	10	0
Oithona similis	369.9	275.0	416.2	32	42	40
O. spinirostris	19.9	16.0	55.5	19	28	31
Corycaeus anglicus	2.8	8.0	3.6	2	10	3

[1]The following species were found in less than five samples: *Calanus plumchrus*, *Gaetanus* immatures, *Paraeuchaeta japonica* immatures, *Candacia bipinnata*, *Eurytemora thompsoni*, *Rhincalanus nasutus*, *Oncaea borealis*, *O. tenella*, *O. media hymena*, *O. mediterranea*, *Sapphirina* sp., and *Microsetella* sp.

TABLE 4.–Total relative density and frequency of occurrence of other holoplanktonic taxa and meroplankton taken within 18 km of the coast during 1969, 1970 and 1971 upwelling seasons. Entries are sums of average abundances at each of four stations.

	Total relative density			Frequency		
Species	1969	1970	1971	1969	1970	1971
Calanus nauplii	119.5	695.5	172.7	21	40	28
Other Copepod nauplii	43.1	68.1	52.3	10	20	20
Amphipods	8.5	18.5	15.7	5	15	14
Euphausiid nauplii	46.3	85.9	84.0	5	26	18
Euphausiid calyptopis	13.3	14.5	17.2	4	17	11
Euphausiid furcilia	30.2	13.6	17.7	14	20	10
Thysanoessa spinifera	35.4	4.0	87.3	2	7	11
Evadne nordmanni	73.7	58.9	9.8	17	26	2
Podon leukarti	2.8	115.3	5.2	2	12	1
Pteropods	10.2	24.6	60.6	11	22	35
Chaetognaths	89.4	50.3	30.8	25	33	34
Oikopleura	69.2	85.7	66.5	11	15	21
Ctenophores	6.0	2.5	34.9	7	5	19
Scyphomedusae	22.9	70.9	22.8	13	28	22
Decapod shrimp mysis	142.7	52.6	45.3	16	24	22
Barnacle nauplii	59.3	168.3	231.4	8	32	23
Barnacle cypris	4.4	64.0	8.3	2	19	10
Polychaete post-trochophores	16.2	20.1	21.4	5	23	15
Bivalve veligers	170.5	258.9	68.3	20	40	27
Gastropod veligers	28.9	79.2	42.2	16	33	23
Hydromedusae	6.1	3.2	10.3	2	2	11
Unidentified annelid without parapodia	8.2	23.1	35.8	3	3	16
Pluteus	0	16.0	117.6	0	5	11
Large round eggs (fish)	36.8	25.0	17.8	11	13	12
Small round eggs	[1]870.1	168.7	226.1	10	28	25
Euphausiid eggs, early	55.0	686.1	449.6	11	29	24
Euphausiid eggs, late	70.0	57.5	39.6	2	16	14
Other fish eggs	19.1	35.1	34.3	12	18	18

[1]Biased by a single observation of 760 individuals/m^3.

Only a few of the taxa in these tables had similar average abundances in each season. Some of the taxa can be assigned "good" and "bad" years on the basis of either their abundance or frequency of occurrence in samples. Others cannot be assigned with much confidence. Accordingly, on the basis of frequency of occurrence, 1971 was the "best" year for the following copepods: *Calanus tenuicornis* Dana, *Clausocalanus arcuicornis* Dana, *Ctenocalanus vanus* Giesbrecht s.l. and *Lucicutia flavicornis* Claus. On the basis of abundance, the following categories can be added to the list: *Metridia lucens* Boeck, *O. spinirostris* Claus, the euphausiid *Thysanoessa spinifera* Holmes, the pteropod *Limacina helicina* (Phipps), ctenophores, hydromedusae, echinoderm pluteus larvae, and unidentified annelids. Using the same criteria, 1971 was the poorest year for the copepods *Paracalanus parvus* Claus, *Pseudocalanus*, *Aetideus pacificus* Brodskii, *Centropages abdominalis*, *Acartia clausii*, *A. tonsa* Dana, *Tortanus discaudatus* Thompson and Scott, and *Epilabidocera longipedata* Sato (= *E. amphitrites* McMurrich). Also poorly represented in 1971 were the cladoceran *Evadne normanni* (Loven) and bivalve mollusc veligers.

A definite pattern emerges from the above classifications. All of the copepod species having their best year in 1971 are basically offshore, warmwater species that can always be found well off the Oregon coast (Peterson and Anderson 1966; Peterson 1972) and which seem to have their highest abundances to the south (Fleminger 1967). Those species which had their poorest year in 1971 are all nearshore, coastal species. In fact, some of the neritic species which had their "best" years in 1969 or 1970 did not even occur in 1971 (*Epilabidocera longipedata*, *T. discaudatus*, and *A. tonsa*; see Figure 6). Fleminger (1967) listed *Paracalanus parvus* and *A. tonsa* as temperate-subtropical neritic, and *Pseudocalanus*, *A. clausii*, *T. discaudatus*, and *E. longipedata* as boreal-temperate neritic. *Centropages mcmurrichi* is also a boreal neritic species (Cameron 1957). The attribute shared by each of the animals having a "poor" year in 1971, is restriction to the neritic zone. Warmwater or cold-water affinities seem unimportant. Even though surface temperatures were much higher in 1971, two important animals with norther affinities and not narrowly restricted to the neritic zone, maintained the same level of abundance as they had in 1969 and 1970: *A. longiremis* and *O. similis*.

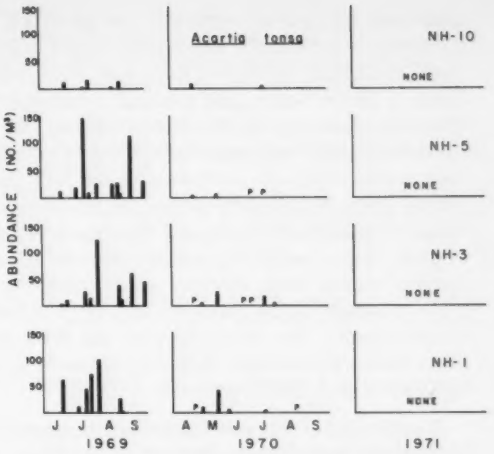


FIGURE 6.—Density of *Acartia tonsa* at NH 1, NH 3, NH 5, and NH 10 in the upwelling seasons of 1969, 1970, and 1971.

There are important differences between the good upwelling years of 1969 and 1970. A number of taxa were very abundant only in 1970: the copepods *Microcalanus pusillus* Sars and *A. clausii*, *Calanus* nauplii, the cladoceran *Podon leukarti* (Sars), barnacle cypris, and gastropod veligers. The year 1969 was the better year for two dominant copepod species (*Calanus* sp. and *Pseudocalanus* sp.), for the copepods *Eucalanus bungii* Giesbrecht and *A. tonsa*, and for shrimp larvae. We do not fully understand these observations.

The greatest share of the taxa listed in Tables 3 and 4 seem to be either equally abundant over all three upwelling seasons (copepod nauplii, euphausiid life history stages, *Oikopleura* sp., polychaete post-trochophores, small round eggs, euphausiid eggs, and fish eggs), or have uncertain or no relationship to the upwelling seasons. These animals include the copepods *Clausocalanus pergens* Ferran, *Scolecithricella minor* Brady, *Metridia pacifica* Brodskii, *Racovitzanus antarcticus* Giesbrecht s.l., *Gaidius* sp., and chaetognaths, barnacle nauplii, and scyphomedusae.

DISCUSSION

Upwelling along the Oregon coast was relatively weak in 1971. It was seldom strong enough to create the low temperature-high salinity conditions close to the beach that are characteristic of the process. This occurred because there were no

sustained periods of southward wind in 1971. There were only four "upwelling events": 2-10 May, 16-25 May, 20 June-2 July, and 10-24 July. Each of these events was unusual compared to those of other years in that the wind also had a substantial eastward component. There were also four storms from the southwest of the sort that characterize the winter period on the Oregon coast: 11-15 May, 16-23 June, 7-9 July, and 27-31 August. It is expected that under these conditions surface waters from offshore would have been more prevalent in the nearshore zone in 1971 than in other years. The composition of the plankton observed in 1971 within 18 km from shore is in agreement with that hypothesis.

Comparison of onshore-offshore hydrographic sections for upwelling events and for intervals of low southward winds (Smith 1974) suggests an explanation for the fact that NH 10 does not show the same degree of year-to-year variations as stations nearer shore. During the upwelling season all isopycnals below 15 m slope upward toward the shore at least as far seaward as 30 km. Upward sloping extends to the shore during upwelling events, but during lapses of the southward wind the isopycnals come to slope downward toward shore from 10 km seaward to the beach. Seaward of 10 km they continue to slope upward despite prolonged lapses. It seems likely that coastal upwelling only takes the form of pulsed events in this most inshore zone. Thus it is reasonable that the low frequency and amplitude of upwelling events in 1971 only had a pronounced effect on the planktology at stations less than 10 km from shore. On the other hand, Hubbard and Pearcy (1971) demonstrated marked changes in the species composition of the salp fauna off Oregon at distances beyond 28 km from shore in 1963, another year of anomalously low coastal upwelling (Bakun 1973). The detailed relationship between inshore and offshore plankton changes as correlated with year-to-year weather variations cannot yet be deduced. The length, frequency, and spatial extent of the data set necessary to deal with this problem probably puts it beyond our reach.

There is a suggestion in the data that intense upwelling events rather immediately result in high zooplankton abundance at the NH 1 and NH 3 stations. Huge population peaks on 10, 18, and 25 July 1969 and 23 June and 2 July 1970 were associated with periods of intense upwelling. The high density found on 22 June 1969, however, followed a 41-day period of little or no north wind. It seems most likely that peak densities are simply reached at about the same time each year, namely late June and early July. We do not as yet know the relationship between copepod developmental schedules and the seasons in this area well enough to decide this issue with any certainty. Further analysis of our data as it bears on this point is planned.

Summers of below average upwelling like 1971, together with the resultant reductions in primary and secondary production, probably have important effects upon nearshore fisheries. A statistical link exists between summer upwelling strength and Dungeness crab production (Peterson, 1973). A strong upwelling season results in a heavy crab catch 1½ yr later. The Dungeness crab catch for the 1972-1973 season was one of the lowest on record.

Other fisheries seem to have been similarly affected. The Fish Commission of Oregon has documented 1971 as a poor growth year for the shrimp *Pandalus jordani* (Robert L. Demory, Oregon Fish Commission, Newport, Ore., pers. commun.), coho salmon, *Oncorynchus kisutch* (Paul H. Reed, Oregon Fish Commission, Newport, Ore., pers. commun.), and razor clams *Siliqua patula* (C. Dale Snow, Oregon Fish Commission, Newport, Ore., pers. commun.). The shrimp data are mean carapace length of Age I animals from the Coos Bay, Ore. area (lat. 43°15′N) and are as follows: 1969, 16.45 cm; 1970, 16.76 cm; and 1971, 15.87 cm. Averaged dressed weights of coho salmon were 2.59 kg in 1969, 3.41 kg in 1970, and 2.68 kg in 1971. Razor clam lengths averaged 75.4 mm in 1969, (no data for 1970), 69.4 mm in 1971, 78.5 mm in 1972, and 83.5 mm in 1973. Some of these data may be better interpreted in terms of good growth years. As shown by the wind data (Figure 3), 1970 had many more days of upwelling inducing winds than 1969. Primary and secondary production should have been greater in 1970. Both shrimp and coho salmon were larger in 1970. Unfortunately no razor clam data were taken in 1970, but data for other years support the conclusion that 1971 was a poor growth year.

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LITERATURE CITED

BAKUN, A.
1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671, 103 p.

BOURKE, R. H.
1972. A study of the seasonal variation in temperature and salinity along the Oregon-Northern California Coast. Ph.D. Thesis, Oregon State Univ., Corvallis, 107 p.

BURT, W. V., AND B. WYATT.
1964. Drift bottle observations of the Davidson Current off Oregon. *In* K. Yoshida (editor), Studies on oceanography, p. 156-165. Univ. Tokyo Press, Tokyo.

CAMERON, F. E.
1957. Some factors influencing the distribution of pelagic copepods in the Queen Charlotte Islands area. J. Fish. Res. Board Can. 14:165-202.

COLLINS, C. A., C. N. K. MOOERS, M. R. STEVENSON, R. C. SMITH, AND J. G. PATTULLO.
1968. Direct current measurements in the frontal zone of a coastal upwelling region. J. Oceanogr. Soc. Jap. 24:295-306.

CROSS, F. A.
1964. Seasonal and geographical distribution of pelagic copepods in Oregon coastal waters. M.S. Thesis, Oregon State Univ., Corvallis, 73 p.

CROSS, F. A., AND L. F. SMALL.
1967. Copepod indicators of surface water movements off the Oregon coast. Limnol. Oceanogr. 12:60-72.

FLEMINGER, A.
1967. Distributional atlas of calanoid copepods in the California Current Region. Part 2. Calif. Coop. Oceanic Fish. Invest., Atlas 7, 213 p.

FROST, B. W.
1974. *Calanus marshallae* a new species of calanoid copepod closely allied to the sibling species *C. finmarchicus* and *C. glacialis*. Mar. Biol. (Berl.) 26:77-99.

HEBARD, J. F.
1966. Distribution of Euphausiacea and Copepoda off Oregon in relation to oceanographic conditions. Ph.D. Thesis, Oregon State Univ., Corvallis, 85 p.

HUBBARD, L. T., AND W. G. PEARCY.
1971. Geographic distribution and relative abundance of Salpidae off the Oregon coast. J. Fish. Res. Board Can. 28:1831-1836.

HUYER, A.
1974. Observations of the coastal upwelling region off Oregon during 1972. Ph.D. Thesis, Oregon State Univ., Corvallis, 149 p.

LAURS, R. M.
1967. Coastal upwelling and the ecology of lower trophic levels. Ph.D. Thesis, Oregon State Univ., Corvallis, 121 p.

LEE, W.
1971. The copepods in a collection from the southern Oregon coast, 1963. M.S. Thesis, Oregon State Univ., Corvallis, 62 p.

PATTULLO, J., AND W. DENNER.
1965. Processes affecting seawater characteristics along the Oregon coast. Limnol. Oceanogr. 10:443-450.

PETERSON, W. K.
1972. Distribution of pelagic Copepoda off the coasts of Washington and Oregon during 1961 and 1962. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River Estuary and adjacent ocean waters, p. 313-343. Univ. Wash. Press, Seattle.

PETERSON, W. K., AND G. C. ANDERSON.
1966. Net zooplankton data from the Northeast Pacific Ocean: Columbia River effluent area, 1961, 1962. Univ. Wash. Tech. Rep. 160, 225 p.

PETERSON, W. T.
1973. Upwelling indices and annual catches of Dungeness crab, *Cancer magister*, along the west coast of the United States. Fish. Bull., U.S. 71:902-910.

PILLSBURY, R. D.
1972. A description of hydrography, winds, and currents during the upwelling season near Newport, Oregon. Ph.D. Thesis, Oregon State Univ., Corvallis, 163 p.

SMITH, R. L.
1974. A description of current, wind, and sea level variations during coastal upwelling off the Oregon coast, July-August 1972. J. Geophys. Res. 79:435-443.

USE OF OTOLITHS TO SEPARATE JUVENILE STEELHEAD TROUT FROM JUVENILE RAINBOW TROUT[1]

J. T. RYBOCK[2], H. F. HORTON[2], AND J. L. FESSLER[3]

ABSTRACT

Otolith nuclei were investigated as a means of separating juvenile steelhead trout, *Salmo gairdneri*, from juvenile rainbrow trout, *S. gairdneri*, in the lower Deschutes River, Oreg. An intensive recreational fishery necessitated development of a technique for differentiation so that impact of the fishery on each race could be assessed independently.

Investigations of adults and hatchery-reared young of *S. gairdneri* revealed that otolith nuclei of steelhead are significantly larger than those of rainbow, size of otolith nuclei does not change with growth of either race, and there are no differences in size of otolith nuclei due to sex or origin (wild vs. hatchery). Thus, size of otolith nuclei provides a means to differentiate effectively juvenile steelhead trout and juvenile rainbow trout regardless of sex or origin. Results also indicated that steelhead mature at a larger size than rainbow, egg size is directly related to body size of dam in both races, and size of otolith nuclei is likely determined by egg size.

This paper reports on an investigation of growth characteristics of the sagittae, the largest of the otoliths, as a means to separate juvenile steelhead trout, *Salmo gairdneri*, from juvenile rainbow trout, *S. gairdneri*. The technology for such differentiation is presently lacking but is necessary for independent management of the two races in streams where they coexist. In the lower Deschutes River, Oreg., for example, the most intensive fishery for rainbow trout occurs during the first week in May when most steelhead smolts migrate; consequently, the catch may be composed of 22-80% juvenile steelhead (King 1966; Wagner and Haxton 1968). Precise knowledge of this catch composition at various locations and times would allow fisheries managers to manipulate fishing pressure so that most steelhead smolts escape capture during migration.

Previously, otoliths have been used to differentiate stocks and races of salmonids. Kim (1963) found differences in the appearance and size of growth rings between spawning groups of sockeye salmon, *Oncorhynchus nerka*. The study most relevant to our investigation demonstrated that winter and summer races of steelhead trout can be separated on the basis of differences in size of the otolith nucleus (ON) (McKern et al. 1974).

The latter authors found that the otolith nucleus is formed early in steelhead trout embryos when all or a great part of nutrition comes from the yolk, and that ON size appears to be directly related to egg size. Also, egg size and fish length of salmonids are often directly related (McFadden et al. 1965; Bulkley 1967; Galkina 1970), and steelhead trout are generally larger than rainbow trout at maturity. Therefore, we hypothesized that steelhead ON are sufficiently larger than rainbow ON to permit separation of juveniles of both races.

We investigated this hypothesis via two series of observations. In the first, an indirect test of validity of the hypothesis, we compared measurements of ON of fish of known race and then determined whether these measurements changed with growth of fish or whether they were related to sex or origin. In the second series, we measured body size of adult fish, egg size of ripe dam, and ON size of fry hatched from these eggs, to determine if correlations between these variables logically accounted for differences in ON sizes. All investigations were conducted on adults and hatchery-reared fingerlings of summer steelhead trout and resident rainbow trout captured in 1971-73 from the lower Deschutes River.

METHODS AND MATERIALS

Study Area

The study area was the lower 100 miles of the

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Deschutes River in north central Oregon (Figure 1). The Deschutes River drains approximately 10,400 square miles, or nearly 11% of the land area of Oregon. Its western tributaries stem from the Cascade Mountains, while eastern tributaries drain Oregon's high plateau. Regulated river flows below Pelton Dam average from 3,000 to 7,100 cfs. Important sport fish in the area include resident rainbow trout, summer steelhead trout, and chinook salmon, *O. tshawytscha*, (Montgomery 1971).

Collection of Samples

Otoliths were obtained from adult (≥200 mm fork length [FL]) rainbow and steelhead (n = 101) sampled during routine Oregon Wildlife Commission creel censuses at Webb's access road (at Buck Hollow Creek) and near Maupin (Figure 1) during August and September 1971 and 1972. Otoliths were removed with a punch described by McKern and Horton (1970). Each fish was measured (FL) and scales (ca. 20) were removed from an area below the origin of the dorsal fin and just above the lateral line. Race was determined from a combination of coloration, relative size, and analysis of scales (Maher and Larkin 1954). In most cases sex was determined from jaw conformation and opercular coloration (steelhead only), and occasionally from fisherman's observations if the fish had been cleaned. To determine origin, we examined steelhead for hatchery marks; hatchery-reared rainbows were distinguished by worn or rounded fins, excessive number of missing scales, and other abnormalities.

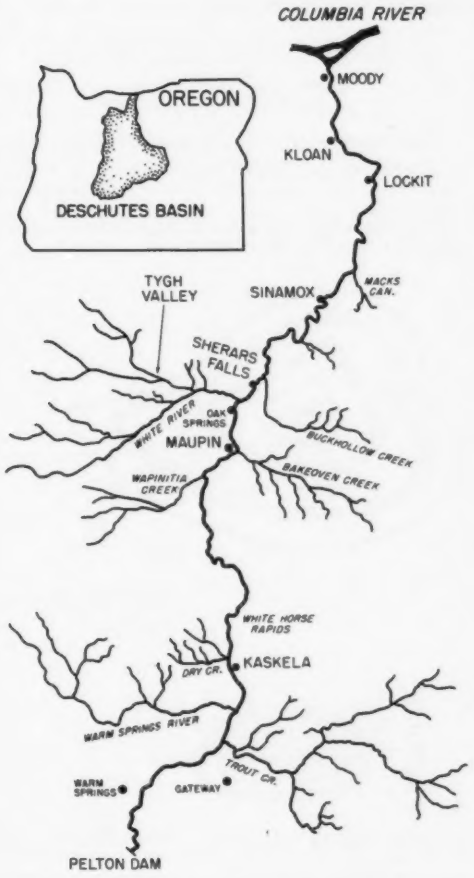

FIGURE 1.—Map of study area on the lower 100 miles of the Deschutes River, Oreg.

Other adult fish (n = 92) were collected by electrofishing near Maupin, below Pelton Dam, and in Bakeoven and Trout creeks (Figure 1) in April-June 1971 and August 1972. Each fish was measured (FL), and race, sex, and origin were determined as above. Otoliths were removed by dissection.

In January 1973, 52 steelhead fingerlings were obtained from the stock of Deschutes River steelhead reared at Wizard Falls Hatchery (Oregon Wildlife Commission) on the Metolius River. These fish represented a random assortment of the offspring of ca. 150 females captured below Pelton Dam. Fork lengths were measured, and otoliths were removed by dissection.

To determine body lengths of mature steelhead trout and rainbow trout, specimens were obtained by electrofishing in the lower Deschutes River in 1972. Fork lengths were measured, and race was determined from hatchery marks or coloration (migrating summer steelhead are more silvery than resident rainbow).

For determination of ova size, adult steelhead were captured in late winter 1972 by trapping below Pelton Dam and were held in tanks until ripe. Twenty-two females were measured (FL), and a sample of eggs (ca. 100) was collected from each fish, fertilized, and allowed to water harden 8-22 h. From 20 to 60 eggs from each pairing were then measured volumetrically (10^{-2} ml) in a 25-ml burette.

Rainbow trout were captured in spring 1972 by electrofishing in the main stem of the Deschutes River. Male-female pairs were individually

spawned, and, after water hardening, the eggs were transported to a laboratory in Corvallis to be hatched. Shortly after arrival, 20 eggs from each of 13 matings were measured as above. Fork lengths were later determined from the frozen dams and sires.

To obtain samples for determination of possible correlation between egg size and ON size of the hatched fry, we randomly selected 10 fingerlings from each of eight available matings of rainbow trout individually hatched and reared in Corvallis (above). Fork lengths were measured, and otoliths were removed by dissection.

Storage and Treatment of Otoliths

The enveloping membrane (sacculus) was removed from each otolith prior to storage. Initially, otoliths were stored dry in coin envelopes before transfer to a clearing solution. Because this method led to breakage of otoliths, later samples were placed in a clearing solution immediately after removal from the fish. Otoliths were cleared from 1 to 21 mo before examination; there was no apparent relationship between clearing time and readableness of the otolith.

Samples were initially cleared in methyl salicylate. Because some otoliths did not clear sufficiently, a 50:50 mixture of glycerin and water (McKern et al. 1974) was used for the remainder of the samples, but this solution tended to increase the opacity of the entire otolith. Neither burning these otoliths on an asbestos pad over a bunsen burner nor clearing the otoliths in oil of cloves increased contrast between the opaque and hyaline parts. Consequently, it was difficult to discern the nucleus.

Improved readings were obtained by applying drops of HCl to the medial surface of otoliths preserved in glycerin and water; this resulted in a dissolution of the medial lobes, a consequent thinning of the otolith, and clearer definition of density patterns. This method is quick (a few milliliters of HCl applied for 2-4 min for a large otolith) and is easily controlled by periodic inspection of the otolith during treatment. Because the edges of the otolith are dissolved, this method should not be used when age determinations are required.

Terminology and Examination of Otoliths

When viewed under reflected light on a black background, the ON of *S. gairdneri* is hyaline with a narrow opaque ring around the border (Figure 2). The metamorphic check is a narrow hyaline ring delineating the nucleus (Kim and Koo 1963). For examination, otoliths were placed lateral surface up on black Plexiglas[4] depression plates, illuminated with a beam of light at 45° and photographed on 35-mm film through a microscope at 50×. Panatomic-X film (ASA 32) was used, and the negatives were enlarged to 4×5 or 5×7 inches onto grade 3 or 4 (high contrast) paper. A stage micrometer was also photographed and enlarged at the same magnifications so that otolith measurements could be determined from the photographs. The length and width of the nucleus (Figure 2) was measured from the photographs by using a compass and the corresponding photograph of the micrometer.

RESULTS AND DISCUSSION

Size of Otolith Nucleus

The linear correlation between ON length and width was strong in both rainbow trout ($r = 0.838$)

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

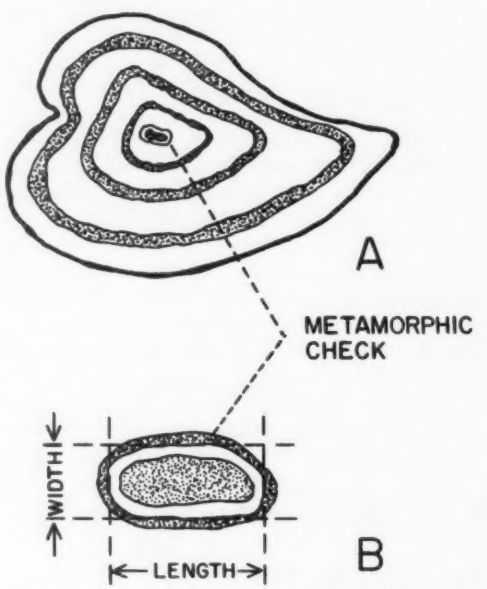

FIGURE 2.–Illustration of (A) otolith and (B) otolith nucleus of *Salmo gairdneri*, with notation of measurements and terminology used.

and steelhead trout (r = 0.916). Neither seemed easier to read. Primarily due to problems of developing methodology, 189 ON (29% of 641 examined) were not sufficiently distinct to permit measurement. Usually, the hyaline center of the nucleus was visible, but the metamorphic check could not be distinguished. Because measurement of the larger dimension would likely be more precise than widths, ON length was used in the following analyses.

The mean ON lengths of steelhead trout (0.354 mm; n = 114) and rainbow trout (0.245 mm; n = 145) differed significantly ($P \leq 0.001$). The length-frequency plot of these data (Figure 3A) demonstrates an overlap of lengths. Most unexpected in this plot are the nucleus lengths for steelhead less than 0.26 mm. These values occur in direct proportion to the values for rainbow; also, these steelhead are from Wizard Falls Hatchery, where both rainbow and steelhead are reared. Perhaps these fish are rainbow offspring which were inadvertently mixed with steelhead during hatchery operations or hybrids of the two species. The length-frequency plot of steelhead ON excluding those from Wizard Falls Hatchery increased the normality of the histogram (Figure 3B); the nadir

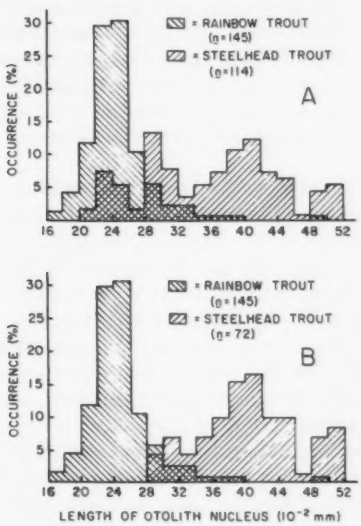

FIGURE 3.—Length-frequency distribution of otolith nuclei of (A) rainbow trout and all steelhead trout and (B) rainbow trout and steelhead trout excluding those from Wizard Falls Hatchery. All fish were captured from the lower Deschutes River, Oreg., 1971-73.

at 0.46-0.48 mm is probably due to the small sample size of each interval. Therefore, although overlap of ON size of the two races occurs between 0.28 mm and 0.34 mm, the race of most juvenile *S. gairdneri* from the Deschutes River can be determined reliably on the basis of this measurement.

The histogram for rainbow more closely approximates a normal distribution, probably the result of a larger sample size and of the many sources of variation operating within a more narrow size range of spawning fish. The ON length of one adult rainbow was 0.48 mm. Although no hatchery marks were noticed, scale characteristics suggested a hatchery origin; because we have observed that almost all hatchery-reared rainbow succumb to *Ceratomyxa* before reaching maturity in the lower Deschutes River, this may have been a nonmigratory steelhead. In general, though, data from our samples do not support the suggestion of Wagner and Haxton (1968) that there may be a great number of such nonmigrants in the Deschutes River.

To determine whether size of ON changes during growth of fish, we regressed length of ON against FL of fish: For rainbow, r = 0.060. For all steelhead, r = 0.694; however, if Wizard Falls fish are excluded, r = 0.018. Even with this exclusion, a wide range of steelhead FL (504-762 mm) was tested; and if the relationship was strong it should have been noticeable in these data.

Mean length of ON was 0.339 mm for all females and 0.317 mm for all males; they are not significantly different ($P \geq 0.20$). Also, the data suggest no significant male-female difference within either race.

Mean length of ON of wild steelhead (0.395 mm; n = 52) was not significantly different ($P \geq 0.20$) from that of hatchery-reared steelhead excluding those from Wizard Falls Hatchery (0.405 mm; n = 20). A similar comparison between adult hatchery-reared and wild rainbow cannot be made since there are few, if any, adult hatchery-reared rainbow in the lower Deschutes River (as mentioned earlier, hatchery fish released in spring succumb to *Ceratomyxa* by summer).

Fish, Egg, and ON Size Relationships

The lengths of rainbow trout and steelhead trout from the lower Deschutes River are distributed into discrete size ranges (Figure 4). Although these fish are not necessarily ready to

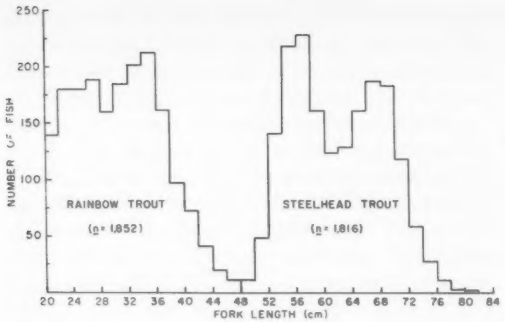

FIGURE 4.–Length-frequency distribution of mature (>20 cm) rainbow trout and steelhead trout from the lower Deschutes River, Oreg., 1972.

spawn, the data indicate low likelihood of significant overlap in length of mature rainbow and steelhead trout.

The mean egg size of steelhead (0.0936 ml) was significantly greater ($P \leq 0.001$) than that of rainbow (0.0727 ml). Also, mean egg size was strongly correlated with length of female (r = 0.829 and 0.791 for rainbow and steelhead trout, respectively) (Figure 5), although there was much variability of mean egg sizes between fish of a similar length and of egg sizes from any one female. For some fish, the largest egg was twice the size of the smallest.

The above r values between body size of dam and egg size are higher than those reported in many other investigations. Scott (1962) measured FL and egg weight of rainbow trout and found no significant correlation. Considering the narrow range of FL (231-264 mm) and the great variability of egg size within length classes, his

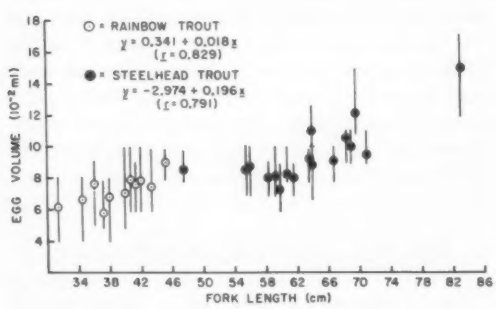

FIGURE 5.–Means and ranges of egg size plotted against length of dam for rainbow trout and steelhead trout from the lower Deschutes River, Oreg., 1972.

results are not surprising. Galkina (1970) found that length of rainbow trout, *S. irideus*, was not highly correlated with mean egg weight (r = 0.48). Although eggs of average size were found in all his females, the smallest eggs were obtained only from smaller females and vice versa. McFadden et al. (1965) found a higher correlation (r = 0.73) between egg size and length of brown trout, *S. trutta*. Blaxter (1969), Galkina (1970), and Lindsey and Ali (1971) cited numerous authors who examined this relationship in many species of fish; although most authors reported a wide range of egg sizes in females of similar length, there is general agreement that a direct, and often high, correlation exists between egg size and dam size.

The presence or absence of any correlation between egg size and ON size of the hatched fish could not be determined directly for the rainbow trout groups reared in Corvallis (egg size had been measured for only four of the eight females whose offspring were available, and we considered this sample size too small). However, since there was a high correlation between egg size and length of dam (r = 0.829), this latter measurement was regressed against ON size of offspring from the eight matings (Figure 6). The r value of 0.489 and the overlap of ranges indicate the relationship is not strong; however, it is a positive correlation. Also, the small sample size (8), the narrow range of dam lengths (295-415 mm), the variation of egg size within any dam, and the substitution of FL for egg size are factors which may have obscured the real extent of the relationship of fish size to ON size.

In summary, we found that because steelhead ON are larger than rainbow ON, size of ON does not change with growth of either race, and correlations of ON size between dams and sires and between wild and hatchery-reared fish of either race are insignificant, ON size is an effective means of differentiating juvenile steelhead trout and juvenile rainbow trout regardless of sex or origin. We also concluded that because steelhead trout are larger at maturity than rainbow trout and because egg size is a direct function of body size, eggs of steelhead trout are larger than those of rainbow trout; and although we did not conclusively demonstrate that ON size is directly related to egg size, other evidence was offered to support the hypothesis that larger egg size was the mechanism responsible for larger ON size in steelhead trout as compared to rainbow trout.

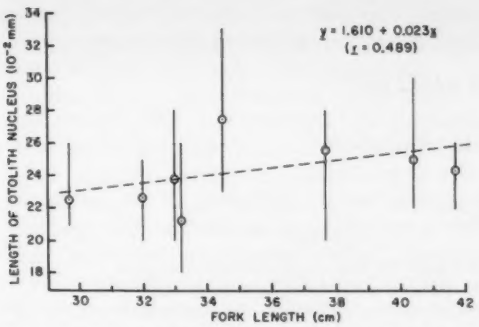

FIGURE 6.—Regression of length of rainbow trout dam from the Deschutes River on length of otolith nucleus of offspring cultured in Corvallis, Oreg., 1972. (Circles are means, and vertical bars are ranges of observation.)

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LITERATURE CITED

BLAXTER, J. H. S.
1969. Development: eggs and larvae. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology 3:117-252. Academic Press, N.Y.

BULKLEY, R. V.
1967. Fecundity of steelhead trout, *Salmo gairdneri*, from Alsea River, Oregon. J. Fish. Res. Board Can. 24:917-926.

GALKINA, Z. I.
1970. Dependence of egg size on the size and age of female salmon [*Salmo salar* (L.)] and rainbow trout [*Salmo irideus* (Gib.)]. J. Ichthyol. 10:625-633.

KIM, W. S.
1963. On the use of otoliths of red salmon for age and racial studies. M.S. Thesis, Univ. Washington, Seattle, 63 p.

KIM, W. S., AND T. S. Y. KOO.
1963. The use of otoliths for age determination in red salmon Univ. Wash., Fish. Res. Inst., Coll. Fish., Contrib. 147:17-19.

KING, D. N.
1966. Deschutes River summer steelhead. Oreg. State Game Comm., Cent. Reg. Adm. Rep. 66-3, 41 p.

LINDSEY, C. C., AND M. Y. ALI.
1971. An experiment with medaka, *Oryzias latipes*, and a critique of the hypothesis that teleost egg size controls vertebral count. J. Fish. Res. Board Can. 28:1235-1240.

MAHER, F. P., AND P. A. LARKIN.
1954. Life history of the steelhead trout of the Chilliwack River, British Columbia. Trans. Am. Fish. Soc. 84:27-38.

MCFADDEN, J. T., E. L. COOPER, AND J. K. ANDERSON.
1965. Some effects of environment on egg production in brown trout (*Salmo trutta*). Limnol. Oceanogr. 10:88-95.

MCKERN, J. L., AND H. F. HORTON.
1970. A punch to facilitate the removal of salmonid otoliths. Calif. Fish Game 56:65-68.

MCKERN, J. L., H. F. HORTON, AND K V. KOSKI.
1974. Development of steelhead trout (*Salmo gairdneri*) otoliths and their use for age analysis and for separating summer from winter races and wild from hatchery stocks. J. Fish. Res. Board Can. 31:1420-1426.

MONTGOMERY, M.
1971. The Deschutes fishery. Oreg. State Game Comm. Bull. 26(3):3-5, 7.

SCOTT, D. P.
1962. Effect of food quantity on fecundity of rainbow trout, *Salmo gairdneri*. J. Fish. Res. Board Can. 19:715-731.

WAGNER, H., AND J. HAXTON.
1968. Observations on the migration disposition of summer steelhead reared at Oak Springs and Wizard Falls Hatcheries. Oreg. State Game Comm., Res. Div., Prog. Rep., 5 p.

DESCRIPTION OF EGGS AND LARVAE OF YELLOWFIN MENHADEN, *BREVOORTIA SMITHI*[1]

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ABSTRACT

Development of yellowfin menhaden, *Brevoortia smithi*, is described from eggs and larvae reared in the laboratory. Eggs were collected during November 1972 in Biscayne Bay, Florida. Eight embryos and 66 larvae and juveniles ranging from 3.7 to 36.2 mm standard length were used to describe development. Mean egg diameter was 1.27 mm, mean oil globule diameter was 0.15 mm, and mean yolk diameter was 1.07 mm. The perivitelline space averaged 16% of the egg diameter. Length at hatching was about 3.0 mm standard length. Larvae were fed on zooplankton and grew about 0.45 mm per day from the 4th until the 20th day after hatching at 26°C. Morphology, meristics, osteology, and pigmentation are described. Transformation from larvae to juveniles apparently was completed at 20 to 23 mm standard length. During transformation full complements of fin rays were developed, the dorsal fin moved forward, the gut shortened, and the anal fin moved forward. Yellowfin menhaden larvae have some characteristics that serve to distinguish them from larvae of other clupeid genera occupying the same geographic range, and also have some characters that may be helpful to distinguish them from other species in the genus *Brevoortia*.

The yellowfin menhaden, *Brevoortia smithi* Hidelbrand, is one of four species of *Brevoortia* that occur along the Atlantic and Gulf of Mexico coasts of the United States. The biology and systematics of yellowfin menhaden were discussed in detail by Hildebrand (1963) and most recently by Dahlberg (1970). Dahlberg reported that *B. smithi* occurs from North Carolina to Louisiana. Atlantic and Gulf of Mexico populations exist, which apparently are distinct, and the species is uncommon south of West Palm Beach on the Florida Atlantic coast and north of Tampa Bay on the Florida west coast. Although common in parts of its range, yellowfin menhaden are not abundant enough to contribute substantially to commercial menhaden catches (Dahlberg 1970). Reproducing populations apparently are confined to coastal areas of the United States, but Levi (1973) reported some juveniles from the Bahamas. Hybrids of *B. smithi* × *B. tyrannus* on the Atlantic coast and *B. smithi* × *B. patronus* on the Gulf coast commonly occur (Turner 1969; Dahlberg 1970).

Reintjes (1962) artificially fertilized eggs of yellowfin menhaden from Indian River, Fla. He presented a series of photographs and described developing embryos and yolk-sac larvae. Hybrid embryos and yolk-sac larvae of yellowfin menhaden and Gulf menhaden, *B. patronus*, were produced artificially (Hettler 1968), and photographs of these embryos and larvae were published. More recently, Hettler (1970a) reared some yellowfin menhaden larvae from artificially fertilized eggs to 14.9 mm. He illustrated larvae of 7.6 and 11.9 mm total length (TL). Despite the literature on yellowfin menhaden development, no complete series from egg through transformation of larvae to the juvenile stage is available, nor have detailed illustrations been published that would be helpful to distinguish yellowfin menhaden from other similar clupeid larvae. We have reared yellowfin menhaden from naturally spawned planktonic eggs to advanced juveniles and we describe development of these stages in this paper.

Eggs and larvae of other *Brevoortia* species have been described, but only those of the Atlantic menhaden, *Brevoortia tyrannus*, are well known. Mansueti and Hardy (1967) have reviewed published information on Atlantic menhaden development. Suttkus (1956) described larvae of Gulf menhaden 18.9 mm and longer, but smaller specimens are undescribed. The eggs and larvae of finescale menhaden, *Brevoortia gunteri*, have not

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been described. DeCiechomski (1968) has discussed occurrence and photographed eggs and yolk-sac larvae of *Brevoortia aurea* from Argentina.

Using our rearing techniques (Houde 1973b), it was relatively simple to rear yellowfin menhaden from eggs to advanced juveniles. Presumably the other species, including Atlantic and Gulf menhaden, can be reared by similar methods if their eggs can be obtained. It should now be possible to conduct experiments under laboratory conditions, testing environmental factors on development of eggs and larvae of these important commercial species.

METHODS

Collecting Eggs

Naturally fertilized eggs from Biscayne Bay, Miami, Fla. were collected in 1-m diameter, 505-μm mesh plankton nets suspended from the dock of the Rosenstiel School of Marine and Atmospheric Science on 3 November and 26 November 1972. Surface temperatures were 25.4° and 22.7°C on the respective collecting days and salinity was 32-33‰. Yellowfin menhaden eggs were sorted by pipette from the other plankton organisms. The eggs that were sorted were known to be yellowfin menhaden because some of the same type had been hatched and the larvae reared during rearing trials in 1971. A total of 90 eggs on 3 November and 170 eggs on 26 November were placed in rectangular tanks of 38-liter capacity for rearing.

Rearing and Preserving Methods

Rearing techniques were similar to those described by Houde (1973b) and Houde and Palko (1970). For the first 20 days of culture, temperature was controlled at 26° ± 1.0°C. Salinities ranged from 33.5 to 37.0‰ and light was provided by fluorescent fixtures at an intensity of 2,500 lx. Zooplankton, consisting mostly of copepod nauplii and copepodites, collected in a 35-μm mesh plankton net, was fed to larvae for the first 12 days; subsequently *Artemia salina* nauplii were fed in addition to zooplankton. A total of 8 embryos and 66 surviving larvae were preserved in 5% buffered Formalin[1] during the culture period to provide the series used to describe development. Specimens from 3.7 mm to 36.2 mm SL (standard length) were included in the developmental series (Table 1), but many juveniles continued to survive and were reared to lengths of 50-60 mm before experiments were terminated.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Meristics and Morphometrics

Methods for counting and measuring are identical to those used by Houde et al. (1974) for *Harengula jaguana* Poey larvae.

Fin rays were counted in each of the developing fins of unstained larvae (Table 2). Myomeres were counted (Table 3) and examined in relation to the dorsal fin and anus. The following myomere counts were made:

Total myomeres: all myomeres; does not include the triangular area preceding the first myoseptum.
Preanus myomeres: number anterior to the anus.
Postanus myomeres: number posterior to the anus.
Predorsal myomeres: number anterior to the dorsal fin origin.
Postdorsal-preanus myomeres: number between the posterior insertion of the dorsal fin and the anus.

The following measurements were made (Table 1): total length, standard length, preanus length, predorsal length, prepelvic length, head length, snout length, eye diameter, and body depth. All references to lengths of larvae in text are to standard length unless otherwise noted.

Osteology

Sequence of ossification was determined from 10 specimens ranging from 5.2 to 25.3 mm SL. They were cleared with trypsin and stained with alizarin, using the method of Taylor (1967).

DESCRIPTION

Embryos

Eight fertilized eggs from the plankton collections were preserved. The embryos were approximately at the midstage of development at the time of collection. Eggs were spherical, the

TABLE 1.–Specimens of laboratory-reared *Brevoortia smithi* used to describe development. Measurements in millimeters.

Total length	Standard length	Preanus length	Predorsal length	Prepelvic length	Head length	Snout length	Eye diameter	Body depth
4.0	3.7	3.1	—	—	0.46	0.08	0.22	—
4.2	4.0	3.4	—	—	0.60	0.11	0.22	0.38
4.2	4.1	3.3	—	—	0.56	0.09	0.20	0.39
4.3	4.1	3.4	—	—	0.52	0.10	0.24	—
4.3	4.2	3.4	—	—	0.52	0.09	0.24	—
4.4	4.2	3.4	—	—	0.56	0.10	0.19	0.40
4.4	4.2	3.4	—	—	0.54	0.06	0.20	0.37
4.4	4.2	3.5	—	—	0.60	0.08	0.26	—
4.4	4.2	3.6	—	—	0.54	0.08	0.26	—
4.5	4.3	3.5	—	—	0.56	0.07	0.22	0.39
4.6	4.4	3.5	—	—	0.55	0.08	0.22	0.34
4.6	4.4	3.6	—	—	0.56	0.08	0.20	0.40
4.6	4.4	3.6	—	—	0.57	0.08	0.23	0.34
4.6	4.4	3.6	—	—	0.60	0.08	0.22	0.38
4.6	4.4	3.6	—	—	0.61	0.10	0.21	0.42
4.7	4.5	3.7	—	—	0.56	0.06	0.24	—
4.7	4.5	3.8	—	—	0.62	0.09	0.24	0.34
4.7	4.5	3.7	—	—	0.56	0.07	0.24	0.40
4.8	4.6	3.8	—	—	0.56	0.08	0.24	0.36
4.8	4.6	3.8	—	—	0.55	0.08	0.22	0.36
4.8	4.6	3.7	—	—	0.56	0.10	0.24	0.36
4.9	4.7	3.7	—	—	0.60	0.09	0.24	0.42
5.4	5.2	4.3	—	—	0.69	0.11	0.25	0.43
5.5	5.2	4.2	—	—	0.74	0.16	0.24	0.43
5.9	5.7	4.8	—	—	0.72	0.10	0.26	0.43
6.3	6.1	5.0	—	—	0.86	0.16	0.26	0.48
6.7	6.4	5.5	—	—	0.84	0.18	0.27	0.47
7.3	7.0	5.9	—	—	0.93	0.18	0.28	0.50
7.5	7.3	6.1	5.0	—	0.88	0.16	0.34	0.58
7.5	7.2	6.0	4.9	—	0.82	0.12	0.26	0.50
7.7	7.4	6.1	5.0	—	1.04	0.26	0.32	0.56
7.7	7.5	6.2	5.1	—	1.08	0.18	0.36	0.65
7.8	7.4	6.3	4.8	—	1.14	0.20	0.26	0.64
8.8	8.6	7.2	5.7	—	1.28	0.22	0.36	0.72
8.8	8.6	7.1	5.5	—	1.42	0.30	0.42	0.70
8.9	8.6	7.1	5.8	—	1.04	0.23	0.28	0.60
8.9	8.6	7.2	5.0	—	1.16	0.28	0.32	0.56
9.3	8.8	7.6	5.8	—	1.42	0.32	0.40	0.74
9.6	9.2	7.8	6.1	—	1.20	0.34	0.38	0.72
10.0	9.6	8.0	6.2	—	1.36	0.22	0.42	0.73
10.2	9.6	8.1	6.3	—	1.56	0.36	0.42	0.72
10.6	10.2	8.6	6.9	—	1.48	0.32	0.42	0.84
10.7	9.9	8.4	6.4	—	1.68	0.30	0.46	0.80
10.8	10.0	8.4	6.5	—	1.64	0.30	0.44	0.80
11.0	10.1	8.5	6.4	—	1.72	0.34	0.48	0.86
11.1	10.3	8.7	6.8	—	1.80	0.38	0.48	0.92
11.2	10.5	8.9	6.7	—	1.64	0.34	0.48	0.80
11.3	10.3	8.7	6.6	—	1.80	0.34	0.48	0.88
11.8	10.9	9.3	6.8	—	2.04	0.40	0.59	0.94
12.3	11.2	9.5	7.0	—	2.24	0.52	0.64	1.04
12.8	11.3	9.3	6.8	5.5	2.14	0.47	0.60	1.00
13.6	12.1	10.3	7.9	—	2.32	0.47	0.60	1.12
13.7	12.3	10.6	7.7	5.8	2.32	0.48	0.76	1.18
14.2	12.6	10.3	7.7	6.1	2.76	0.56	0.84	1.42
15.2	13.5	10.9	8.4	6.6	3.00	0.66	0.80	1.48
15.6	13.8	11.4	8.4	6.2	2.68	0.52	0.82	1.54
18.0	15.5	12.5	9.2	7.9	4.00	0.83	1.32	2.60
18.0	15.9	13.0	9.2	6.9	3.12	0.68	0.90	1.80
19.1	16.2	12.6	9.2	7.9	4.12	0.86	1.24	2.66
19.5	16.9	13.0	9.3	8.8	4.83	1.00	1.50	3.42
21.1	17.8	13.3	9.4	9.1	5.25	1.20	1.56	3.92
21.2	18.0	14.2	9.5	9.1	5.17	1.25	1.62	4.25
27.1	22.7	16.8	11.7	11.8	7.46	1.67	2.50	6.58
30.1	25.3	18.3	12.5	13.2	7.92	1.90	2.50	7.50
41.2	33.3	23.9	15.7	17.4	11.10	2.31	3.42	10.60
43.9	36.2	26.7	18.0	20.0	12.05	2.74	3.42	11.96

chorion was thin and unsculptured, and they had a single yellowish oil globule. Egg diameters ranged from 1.21 to 1.34 mm (mean = 1.27 mm), and oil globule diameters ranged from 0.12 to 0.17 mm (mean = 0.15 mm). Yolk diameters ranged from 0.80 to 1.19 mm (mean = 1.07 mm) and were large relative to egg diameter. Our egg diameters and oil globule diameters are much like those reported

TABLE 2.—Some meristic characters of laboratory-reared specimens of *Brevoortia smithi*.

Standard length (mm)	Days after hatching	Principal caudal rays	Procurrent caudal rays		Dorsal rays	Anal rays	Pectoral rays	Pelvic rays
			Dorsal	Ventral				
3.7-7.2	0-5	No elements present on 29 specimens in this size range.						
7.3	5	—	—	—	6	—	—	—
7.4	7	—	—	—	7	—	—	—
7.4	5	—	—	—	4	—	—	—
7.5	9	2	—	—	7	—	—	—
8.6	6	2	—	—	6	—	—	—
8.6	5	2	—	—	6	—	—	—
8.6	7	4	—	—	8	—	—	—
8.6	15	3	—	—	12	—	—	—
8.8	9	18	—	—	14	7	—	—
9.2	7	3	—	—	9	—	—	—
9.5	8	17	—	—	11	—	—	—
9.6	9	19	—	—	13	?	—	—
9.9	11	19	—	—	15	10	—	—
10.0	10	19	—	—	14	—	—	—
10.1	16	19	—	—	17	7	—	—
10.2	7	17	—	—	13	—	—	—
10.3	13	19	—	—	16	12	—	—
10.3	11	19	—	—	14	8	—	—
10.5	11	19	—	—	15	9	—	—
10.9	18	19	—	—	16	16	—	—
11.2	18	19	3	2	18	14	—	—
11.3	15	19	2	1	18	18	—	—
12.1	15	19	3	2	17	14	—	—
12.3	20	19	3	2	19	18	—	—
12.6	29	19	4	3	18	20	—	6
13.5	24	19	5	3	18	19	—	6
13.8	24	19	4	3	19	19	—	6
15.5	43	19	7	6	20	21	13	7
15.9	18	19	6	5	17	18	5	4
16.2	28	19	8	6	19	20	13	7
16.9	43	19	7	6	19	20	14	7
17.8	31	19	8	7	20	21	15	7
18.0	38	19	9	8	20	20	14	7
22.7	60	19	8	6	21	21	14	7
25.3	50	19	8	7	20	21	14	7
33.3	176	19	8	7	20	21	16	7
36.2	102	19	8	7	20	20	15	7

TABLE 3.—Distribution of myomeres relative to other body parts for *Brevoortia smithi* larvae.

Length class (mm, SL)	Preanus myomeres			Postanus myomeres			Predorsal myomeres			Postdorsal-preanus myomeres		
	Number of specimens	Range	Mean	Number of specimens	Range	Mean	Number of specimens	Range	Mean	Number of specimens	Range	Mean
3.7- 6.0	24	36-39	37.58	24	7- 9	7.96	—	—	—	—	—	—
6.1- 8.0	8	36-38	37.25	8	7- 9	8.12	4	27-29	28.00	4	5-6	5.25
8.1-10.0	10	35-37	36.20	10	8-11	9.70	10	24-28	26.20	10	4-5	4.60
10.1-12.0	8	33-37	35.38	8	10-13	10.75	8	22-25	24.00	8	3-5	4.00
12.1-14.0	5	33-35	33.40	5	11-13	12.20	5	21-22	21.40	5	3-4	3.40
14.1-16.0	2	30-33	31.50	2	13-15	14.00	2	19-21	20.00	2	2-4	3.00
16.1-18.0	4	29-31	29.75	4	15-16	15.50	4	18-22	19.50	4	2	2.00
>22.7	4	28-29	28.50	4	16-18	17.00	4	15-17	15.75	4	2-3	2.25

by Reintjes (1962) for yellowfin menhaden, but yolk diameters differ greatly. In his specimens the perivitelline space averaged more than 30% of the egg diameter, but in our specimens it averaged only 16%. The difference might be partly accounted for by the incubation salinities. Salinities at Indian River where Reintjes did his study were relatively low, ranging from 20.5 to 27.2‰, while those in Biscayne Bay during our study exceeded 32‰. Hettler (1968) also reported narrow perivitelline spaces in hybrid eggs from *B. smithi* × *B. patronus* that he artificially fertilized at the collection site where salinities were 33-34‰. Previtelline spaces in his embryos ranged from 7 to 17% of the egg diameters, and he attributed the narrow spaces to possible effects of high salinity. Yellowfin menhaden eggs have been collected by us from Biscayne Bay on many occasions in 1971 to 1973, and they always are characterized by a relatively narrow perivitelline space, which is unusual

for clupeid species that spawn in South Florida marine waters.

Developing embryos resembled those described and photographically illustrated by Reintjes (1962). On our preserved specimens, tiny melanophores were present only on the dorsal surface of the developing embryo. The yolk mass was segmented, but this was observed with difficulty in preserved material. No pigment was observed on the yolk sac or oil globule of our preserved eggs.

Spawning by yellowfin menhaden in Biscayne Bay occurred at least between November and February. Spawning by this species has not been reported previously in Biscayne Bay, but eggs were common during 1971-73. We do not know the time of day at which spawning took place or the total incubation time at 22° to 26°C. Hettler (1970b) collected planktonic eggs of yellowfin menhaden in the Indian River and observed that they spawned at dusk. Reintjes (1962) reported hatching in 46 h at 19°C. Since we have collected embryos only in a single stage of development when temperatures were above 22°C, incubation time might be 24 h or less at these temperatures. Eggs were collected between 0900 and 1400 h; hatching in our aquaria was complete before 2400 h.

Description of Larvae

Body Shape and Growth

Larvae were about 3.0 mm SL at hatching. They averaged 4.2 mm SL at 20 h after hatching (Figure 2A) when the body axis had straightened. During the first 2 days after hatching they were similar to yellowfin menhaden larvae described by Reintjes (1962). Larvae resemble those of other clupeid fishes. They are elongate, rod-shaped larvae after the yolk has been absorbed. At transformation they become deeper bodied and more laterally compressed. Proportional measurements of larvae in relation to standard length are summarized in Table 4.

Most larvae did not grow in length from the 1st until the 4th day after hatching at 26°C. Growth was rapid from the 4th until the 10th day (Figure 1), averaging about 0.80 mm/day. Growth was slower and more variable on subsequent days, but averaged about 0.45 mm/day from the 4th until the 20th day after hatching. Our 36.2-mm specimen was preserved 102 days after hatching,

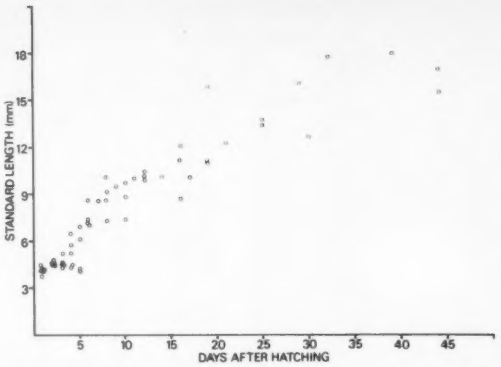

FIGURE 1.–Growth of laboratory-reared larvae of *Brevoortia smithi*.

but growth rate of juveniles was almost certainly lower than might be expected under better feeding conditions because we did not maintain a careful feeding schedule after larvae transformed to the juvenile stage. Several juveniles from 50 to 60 mm were preserved when the experiments were terminated at 235 days after hatching. At 20°C, Hettler (1970a) reported growth rates of about 0.27 mm/day for yellowfin menhaden larvae that he reared for 27 days. The four smallest larvae that we preserved on the 4th and 5th days after hatching were smaller than larvae preserved on previous days (Figure 1). It is probable that those larvae had not begun to feed and that they were starving at the time of preservation.

Yolk Absorption and Gut Differentiation

The yolk sac is broadly ellipsoid in newly hatched larvae with the oil globule located ventrally and just posterior to the middle of the yolk mass (Figure 2A; see also Reintjes 1962). The yolk was nearly absorbed in specimens preserved 1 day after hatching (Figure 2B). All visible yolk remains, including the oil globule, had disappeared by 60 h after hatching at 26°C. Many larvae were observed to begin feeding before all of the yolk had been absorbed. At that time the gut was a straight tube, but within 24 h (at about 5.0 to 5.5 mm SL) it had developed into distinct fore and hind sections, the latter characterized by the bands of muscle common to all clupeid larvae.

Preanus Length

Preanus length averaged 82 to 84% SL from hatching until larvae were 15.0 mm SL (Table 4).

TABLE 4.–Summary of the measurements of various body parts of *Brevoortia smithi* larvae and juveniles in relation to standard length. Tabulated measurements are means for measurements from 1-mm length classes.

Length class (mm, SL)	Number of specimens	Preanus length:SL	Predorsal length:SL	Prepelvic length:SL	Body depth:SL	Head length:SL	Snout length:SL	Eye diameter:SL
3.1- 4.0	2	0.84	—	—	0.09	0.14	0.02	0.06
4.1- 5.0	20	0.82	—	—	0.09	0.13	0.02	0.05
5.1- 6.0	3	0.82	—	—	0.08	0.13	0.02	0.05
6.1- 7.0	3	0.84	—	—	0.08	0.14	0.03	0.04
7.1- 8.0	5	0.84	0.67	—	0.08	0.13	0.03	0.04
8.1- 9.0	5	0.84	0.66	—	0.08	0.15	0.03	0.04
9.1-10.0	5	0.84	0.65	—	0.08	0.15	0.03	0.04
10.1-11.0	6	0.84	0.64	—	0.08	0.17	0.03	0.05
11.1-12.0	2	0.84	0.62	0.49	0.09	0.20	0.04	0.06
12.1-13.0	3	0.84	0.63	0.47	0.10	0.20	0.04	0.06
13.1-14.0	2	0.82	0.62	0.47	0.11	0.21	0.04	0.06
15.1-16.0	2	0.81	0.59	0.47	0.14	0.23	0.05	0.07
16.1-17.0	2	0.77	0.56	0.50	0.18	0.27	0.06	0.08
17.1-18.0	2	0.77	0.53	0.51	0.23	0.29	0.07	0.09
22.7	1	0.74	0.52	0.52	0.29	0.33	0.07	0.11
25.3	1	0.72	0.49	0.52	0.30	0.31	0.08	0.10
33.3	1	0.72	0.47	0.52	0.32	0.33	0.07	0.10
36.2	1	0.73	0.49	0.55	0.33	0.33	0.08	0.09

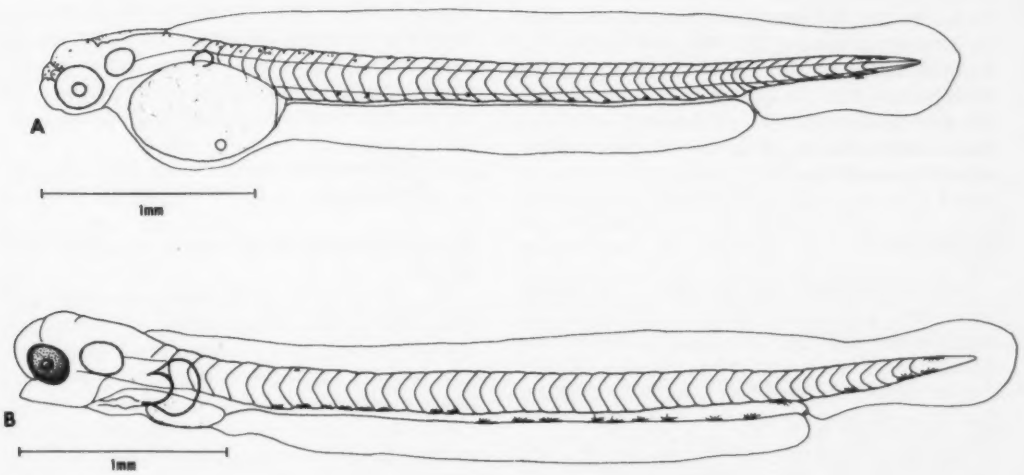

FIGURE 2.–4.2-mm SL (20 h posthatching) and 4.6-mm SL (41 h posthatching) larvae of *Brevoortia smithi*.

As the gut shortened during transformation, preanus length was reduced to 77% SL at 16.0 to 18.0 mm and averaged 72 to 74% for juveniles 22.7 mm and longer.

Head Length

Head length averaged 13 to 14% SL for larvae from 3.0 to 8.0 mm (Table 4). It then increased gradually to 29% at 18.0 mm and stabilized at 31 to 33% SL for juvenile specimens. Hildebrand (1963) and Dahlberg (1970) recorded head lengths ranging from 29 to 32.5% SL for large juvenile and adult yellowfin menhaden.

Eye Diameter

Eye diameter averaged 6% SL on newly hatched larvae but gradually decreased to 4% SL at about 6.0 mm and was stable until larvae grew to 10.0 mm (Table 4). Eye diameter then increased to 9% SL at 18.0 mm and averaged 9 to 11% SL for juveniles 22.7 to 36.2 mm. A relative decrease in eye diameter must occur in older juveniles because

Hildebrand (1963) reported eye diameters ranging from 6.1 to 7.5% SL for specimens 91 mm and longer.

Snout Length

Snout length increased gradually throughout development. It averaged 2% SL at hatching and increased to 7 to 8% SL in our juveniles (Table 4). Snout lengths of large juvenile and adult yellowfin menhaden range from 6.8 to 8.0% SL (Hildebrand 1963).

Body Depth

Body depth, measured at the pectoral symphysis, averaged 8 to 9% SL from hatching until larvae were 12.0 mm (Table 4). A rapid increase in body depth then occurred; it was 23% SL at 18.0 mm and apparently was still increasing in juvenile specimens 22.7 mm and longer. Our 36.2-mm specimen had a body depth of 33% SL. Hildebrand (1963) did not measure body depth by the same method that we used, but he noted that yellowfin menhaden juveniles are deep bodied, more so than adults of this species.

Predorsal Length

Predorsal lengths were measured on larvae that had dorsal fin rays developing. No dorsal fin development was observed on any specimens less than 7.3 mm. Predorsal length decreased gradually from 67 to 62% SL for larvae from 7.3 to 14.0 mm and then decreased more rapidly for larger specimens (Table 4). It was 52% SL for our 22.7-mm specimen and ranged from 47 to 49% SL for larger individuals. The decrease in predorsal length from 67 to 62% for 7.3- to 14.0-mm larvae may be partly due to measuring predorsal length on specimens with incompletely developed dorsal fins. The marked decrease in predorsal length on larger larvae resulted from forward movement of the dorsal fin as larvae began to transform to the juvenile stage.

Prepelvic Length

Prepelvic lengths were measured on larvae that had pelvic fin buds or fins. From 11.1 to 16.0 mm, prepelvic lengths ranged from 47 to 49% SL (Table 4). In larger specimens, prepelvic lengths increased to 51% SL at 18.0 mm and to about 52% SL for 22.7- to 33.3-mm individuals. Our 36.2-mm specimen had a prepelvic length of 55% SL. Pelvic fins moved posteriorly during growth of yellowfin menhaden larvae, causing the observed increase in prepelvic length.

Meristics

Myomeres

The number of myomeres in fishes corresponds approximately to the number of vertebrae. Dahlberg (1970) reported 43 to 46 vertebrae (mean = 45) for juvenile and adult *B. smithi*. Myomeres can be counted on larvae before development of vertebrae and are a valuable meristic character. Total numbers of myomeres in our specimens ranged from 45 to 47 on the 63 individuals for which accurate counts were obtained. There was no correlation between the number of myomeres and standard length, indicating that the full complement was present at hatching. The frequencies of occurrence were as follows:

Number of myomeres	*45*	*46*	*47*
Frequency	26	32	5

The mean number of myomeres was 45.67 ($S_{\bar{x}}$ = 0.1109).

The distribution of myomeres in relation to other body parts can be useful for identifying clupeid larvae (Ahlstrom 1968). We examined the distribution of myomeres for yellowfin menhaden larvae relative to the dorsal fin and anus (Table 3). Preanus myomeres decreased from a mean number of 37.6 in newly hatched larvae to 28.5 in juveniles that were 22.7 mm and longer. Postanus myomeres increased accordingly, from 8.0 in newly hatched larvae to 17.0 for juveniles. Shortening of the gut during development caused the change in distribution of preanus and postanus myomeres. Predorsal myomeres decreased in numbers as larvae developed, because the dorsal fin moved forward. Larvae of 6.1 to 8.0 mm had a mean number of 28.0 predorsal myomeres, but juveniles had only 15.8. Numbers of predorsal myomeres were variable for specimens within any given size class (Table 3). The number of postdorsal-preanus myomeres decreased as larvae grew. Larvae 6.1 to 8.0 mm had a mean number of 5.3 postdorsal-preanus myomeres, but advanced larvae and juveniles always had 4 or fewer (usually 2

or 3). Larvae of *Opisthonema oglinum* and *Harengula jaguana* always had 5 or more post-dorsal-preanus myomeres during all developmental stages (Richards et al. 1974; Houde et al. 1974).

Fin Development

A finfold surrounded the trunk and caudal area of newly hatched yellowfin menhaden larvae. Some parts of it remained along the ventral body margin until larvae were approximately 16.0 mm. Pectoral fin buds were already present when larvae hatched (Figure 2A), but the pelvic and median fins were not formed. Rays first appeared in fins in the following sequence: dorsal, caudal, anal, pelvics, and pectorals. Because rays first develop as cartilaginous structures, the size at which full complements were present was not necessarily the size at which all rays were ossified (Tables 2, 5). Although the beginning and completion of fin ray development were best correlated with length of larvae, age was also a factor, especially for anal fin development (Table 2).

Median fins had full complements of rays when larvae were 17.0 mm (Table 5). Dorsal rays first appeared at 7.3 mm, although an opaque area was present in the dorsal finfold, near the future dorsal fin, in some larvae as small as 6.4 mm. Full complements of 20 or 21 dorsal rays usually were attained when larvae were 15.5 to 17.0 mm. Principal caudal rays first appeared at 7.5 to 8.6 mm and the full complement of 19 principal rays was present when larvae were 9.6 to 10.3 mm. The notochord began to flex while principal caudal rays and other caudal fin structures were developing. Procurrent caudal rays began to develop at 11.2 mm, and full complements of 8 or 9 dorsal and 6 or 7 ventral rays were present at 16.2 to 17.8 mm. Anal rays first developed at 8.8 to 10.3 mm. A full complement of 20 or 21 rays was present on all larvae 16.2 mm or longer, although one specimen only 12.6 mm had 20 anal rays. Hildebrand (1963) and Miller and Jorgenson (1973) reported from 21 to 24 anal rays in yellowfin menhaden specimens longer than 72 mm that they examined. We examined six juveniles from our rearing experiment that were 40-50 mm in length. Two of these specimens had 22 anal rays, two had 21 rays, and two had 20 rays.

Rays in paired fins began to develop later than in median fins. Pectoral fins without rays were present soon after hatching, but no rays developed until larvae had attained approximately 15.5 mm. A full complement of 14 to 16 pectoral rays was present on larvae 16.9 mm and longer. Pelvic fins appeared as tiny buds when larvae were 10.9 to 11.3 mm, but rays did not develop until larvae were about 13.0 mm. A full complement of 7 pelvic rays was attained at 15.5 to 16.2 mm.

Scales and Scutes

Scales and ventral scutes were observed in specimens 17.8 mm and longer. Scales first developed anterior to the dorsal fin and in the region of the caudal peduncle. Specimens 22.7 mm or longer were fully scaled. Ventral scutes first developed anterior to the pelvic fins when larvae were 16.9 mm. Full complements of 30 to 32 (18 to 20 anterior to the pelvic fins and 11 to 13 posterior to the pelvic fins) were present on specimens 22.7 mm and longer. These counts are the same as those given for adult *B. smithi* by Dahlberg (1970).

Osteology

Ten specimens of yellowfin menhaden were cleared and stained to determine sequence of development of skeletal structures. Ossification was similar to that described for larvae of Atlantic thread herring (Richards et al. 1974) and of scaled sardine (Houde et al. 1974). Consequently,

TABLE 5.–Summary of fin development sequence in larvae of *Brevoortia smithi*.

Fin	Buds first appear	Standard length (mm)		Number of rays in fully developed fin
		Rays first appear	Full complement of rays	
Dorsal	—	7.3	15.5 to ~17.0	19 to 21
Caudal:				
Principal	—	7.5 to 8.6	9.6 to 10.3	19
Procurrent	—	11.2	16.2 to 17.8	8 or 9 dorsal 6 or 7 ventral
Anal	—	8.8 to 10.3	12.6 to 16.2	20 or 21
Pelvic	10.9 to 11.3	~12.6	15.5 to 16.2	7
Pectoral	<4.0	~15.5 mm	16.9	14 to 16

[1]Rays were present at the tabulated lengths, but not necessarily ossified at those sizes.

osteology of yellowfin menhaden larvae is treated rather briefly in this paper. Ossification of most structures occurred at a smaller size in yellowfin menhaden than in either Atlantic thread herring or scaled sardines, but the sequence of development was similar in all of the species.

No bones were ossified in our 5.2-mm specimen, but the cleithra were lightly stained in 6.1- and 7.2-mm specimens. Cleithra were well stained in a 7.4-mm specimen, but no other bones were ossified. Slight ossification of the maxillaries and dentaries, in addition to the cleithra, was observed in our 8.6-mm larva. At 10.5 mm, the caudal fin complex began to ossify, cranial bones were lightly stained, and 8 maxillary and 3 dentary teeth were present. Vertebral centra were beginning to stain at 12.3 mm; neural and hemal arches were developing, but were unstained. Dorsal fin rays were ossifying at 12.3 mm. Also, cranial bones were ossifying, the hyoid apparatus was stained, 11 teeth were present on the maxillaries, and 4 were present on the dentaries. At 16.2 mm, most of the major skeletal structures were at least partly ossified. Rays in median and paired fins were stained as were neural and hemal spines along the vertebral column. Premaxillaries and posterior supramaxillaries were ossified in this specimen. At 18.0 mm, the degree of stain uptake increased in most bones. Also, ribs were stained, anterior supramaxillaries were stained, and 16 maxillary teeth were present, but the dentary bore no teeth. Ossification was complete in our 25.3-mm specimen. A total of 25 maxillary teeth but no dentary teeth were present. Dentary teeth are a transient larval character in *B. smithi*. One large, erect tooth was present on the basihyal of our 18.0-mm specimen, and two were present on the 25.3-mm specimen. Basihyal teeth also were reported from Atlantic thread herring and scaled sardine larvae (Richards et al. 1974; Houde et al. 1974).

The caudal fin complex of yellowfin menhaden developed much like that of scaled sardine, and we give a brief description here, using the terminology of Houde et al. (1974) in their description of scaled sardine. Some cartilaginous, principal caudal rays developed in specimens as small as 7.5 mm. Flexure of the notochord and appearance of cartilaginous hypural plate elements occurred at about 8.5 to 9.0 mm. Our 10.5-mm specimen had stain uptake in the proximal parts of the 19 principal caudal rays, and the first uroneural was slightly stained. Hypural elements were present but unstained. At 12.3 mm, the 19 principal caudal rays were fully stained, the second ural vertebra was stained as were the first and second uroneurals, and the parhypural was lightly stained. The hypurals were present but unstained as were two epural bones. Ossification was progressing in our 16.2-mm specimen. Both the first and second ural vertebrae were stained, the six hypurals were stained, the parhypural was well stained, and all three uroneurals were now stained. In addition to the 19 principal caudal rays, 8 dorsal procurrent caudal rays and 6 ventral procurrent caudal rays were stained. Two epurals were present on this specimen but were unstained. At 18.0 mm, all of the bones in the caudal fin area were at least partly ossified. The two epurals were now slightly stained, and 9 dorsal plus 8 ventral procurrent caudal rays were present and stained. The 25.3-mm specimen had all caudal fin bones ossified. The two epurals were well stained on this specimen, these bones being the last to ossify in the caudal fin complex.

Pigmentation

Melanophore distribution on yellowfin menhaden larvae is similar to other clupeid larvae, but there are some distinctive characteristics which may serve to distinguish them from other clupeid larvae with which they can occur. Melanophores were contracted on some specimens and expanded on others, accounting for some of the apparent variability among individuals. Our illustrated specimens (Figures 2-5) have pigment that is typical of most specimens of those lengths.

Head Region

Newly hatched yellowfin menhaden larvae have several tiny melanophores on the snout and a few over the brain. Within 1 day after hatching those melanophores have migrated or disappeared, because no pigment is present on the heads until larvae attain about 9.0 mm. The eyes became pigmented at about 4.5 mm, at 1 day after hatching. Typical pigmentation on the pectoral symphysis and over the heart developed at 4.5 to 6.0 mm. One or two melanophores appeared on the pectoral symphysis after yolk absorption when larvae were 4.5 to 5.0 mm. Those melanophores developed into two distinct pairs by 7.0 mm. Either one or two melanophores developed over the heart at about 6.0 mm. A single melanophore occurred at the

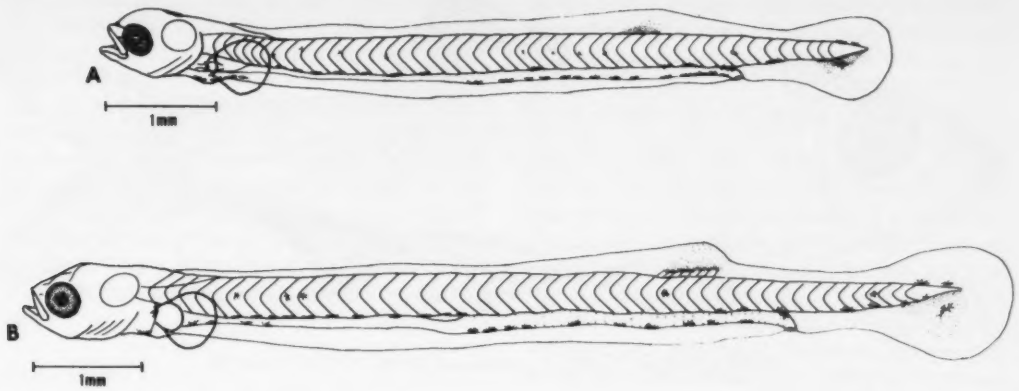

FIGURE 3.—7.0-mm SL (4 days posthatching) and 8.6-mm SL (6 days posthatching) larvae of *Brevoortia smithi*.

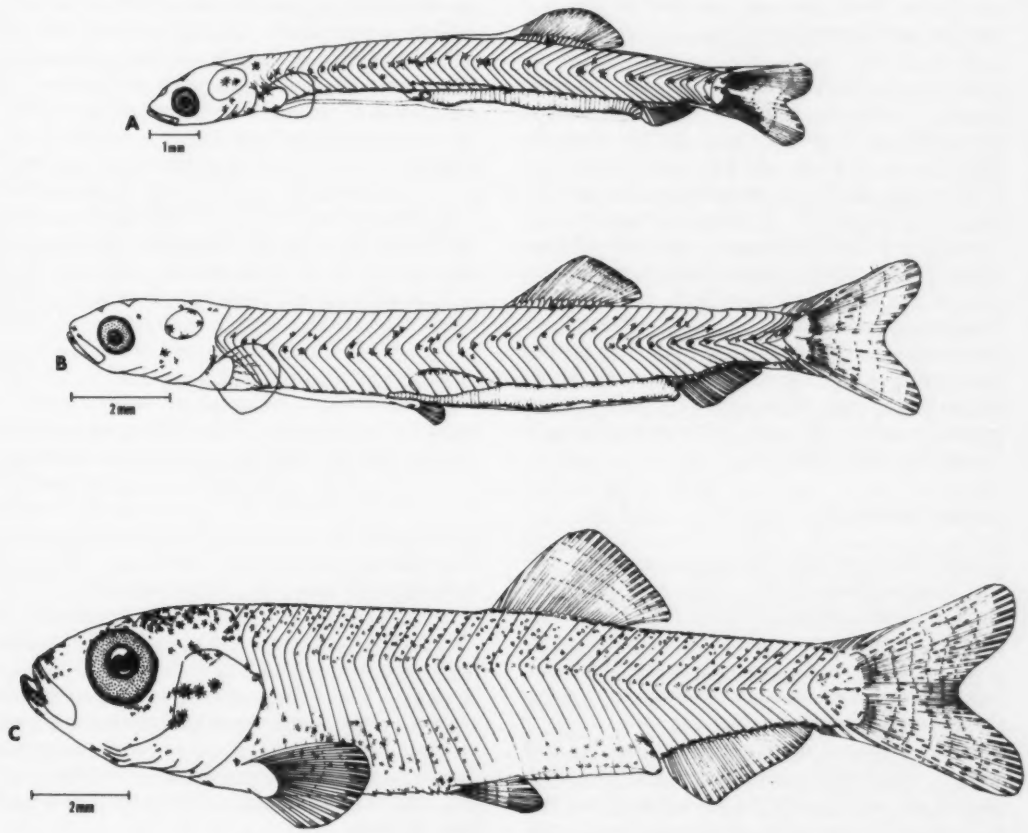

FIGURE 4.—12.1-mm SL (15 days posthatching), 15.9-mm SL (18 days posthatching), and 17.8-mm SL (31 days posthatching) larvae of *Brevoortia smithi*.

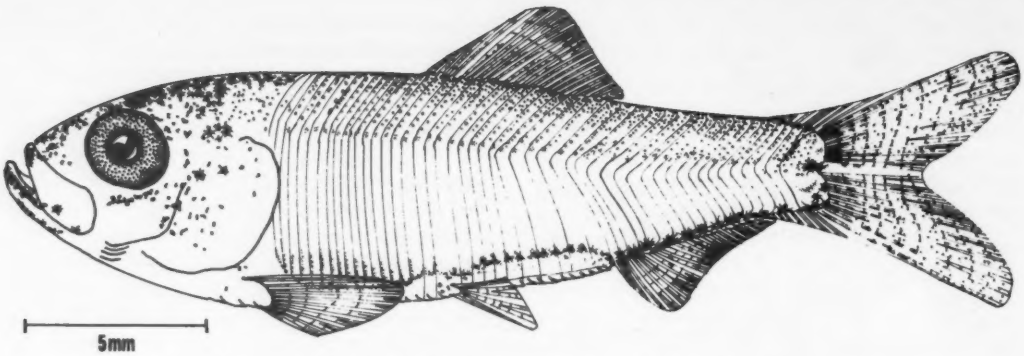

FIGURE 5.—22.7-mm SL (60 days posthatching) juvenile of *Brevoortia smithi*.

pectoral fin base in some larvae as small as 4.5 mm and was present in all larvae at 7.0 mm. The pigment pattern associated with the pectoral symphysis, heart area, and pectoral fin base was retained until larvae were about 16.5 mm.

At 9.0 mm, from one to three stellate melanophores had developed internally and could be seen through the otic capsules. A single, stellate melanophore frequently was present over the hindbrain at 10.0 mm, and some specimens had a small melanophore just posterior to and dorsal to the eye at that length. At about 12.0 mm, the pigmentation on the head began to increase substantially. Melanophores appeared on both jaws, on the side of the head, and over both midbrain and hindbrain regions. The number of melanophores increased as larvae grew, and numerous stellate melanophores were present on the heads of the larvae at 16.5 mm. Melanophores were especially concentrated on the jaws and over the brain in larvae larger than 16.5 mm.

Gut and Trunk Region

Newly hatched yellowfin menhaden had a few tiny melanophores on the dorsal surface of the trunk along the forebody. Within 12 h of hatching, these melanophores apparently migrated ventrally because they disappeared on the dorsal surface, but a series of malanophores was developing along the gut region of larvae.

Paired series of melanophores along the gut margin, which are typical of clupeid larvae, were present on yellowfin menhaden larvae of 4.5 mm and longer. Distinct pairs, numbering from 8 to 16, developed along the dorsolateral margin of the foregut and less distinct pairs, numbering 9 to 14, occurred along the ventral margin of the hindgut. These series were clearly visible until larvae were about 17.0 mm; they were not present on specimens longer than 18.0 mm. From one to three stellate melanophores usually occurred near the anus along the dorsal surface of the gut on larvae longer than 4.5 mm. These were continuous with an internal series of melanophores that were visible over the hindgut on most specimens longer than 8.5 mm. The number in this series increased from 6 to about 17 at 10.5 mm. Three or four melanophores were associated with the developing swim bladder in 10.0- to 12.0-mm larvae. A second internal series of melanophores was associated with developing vertebrae, but these were too indistinct to count accurately.

Pigment developed along the sides of the trunk of some yellowfin menhaden as small as 5.2 mm. From 1 to 3 stellate melanophores were present on some larvae between 5.5 and 7.0 mm, and this number usually increased to as many as 10 for 7.0- to 10.0-mm larvae. Some larvae up to 8.6 mm had no lateral pigment on the trunk, but most specimens, when examined closely, were observed to have these melanophores. The number of lateral melanophores increased greatly when larvae were between 10.0 and 12.0 mm; some specimens of those lengths had as many as 25 lateral melanophores. When larvae were 14.0 mm or longer, these melanophores became very numerous, and most were located above the lateral midline. A paired series of melanophores developed along the dorsal midline, both anterior and posterior to the dorsal fin, on specimens longer than 16.5 mm.

There are melanophores associated with the developing fins. From 1 to 3 stellate melanophores

were present at the dorsal fin base of 9.5- to 11.0-mm larvae. They numbered from 3 to 8 at about 14.0 mm and then as many as 15 at 18.0 mm. Two or three stellate melanophores were present at the anal fin base on 11.0- to 12.0-mm larvae; these numbers increased rapidly to 11 or 12 at 18.0 mm. Numbers of melanophores at the dorsal and anal fin bases were variable among individuals of the same length. A single stellate melanophore developed at the pelvic fin base on specimens as small as 12.3 mm. Some tiny melanophores began to occur in the pectoral, dorsal, and anal fins at 16.2 mm.

Caudal Region

Newly hatched larvae have melanophores on both the dorsal and ventral sides of the notochord tip. Numbers on the dorsal tip range from one to two, while those on the ventral tip range from one to three. In addition, one or two melanophores are located along the ventral midline posterior to the anus. Pigment along the ventral tip of the notochord began to migrate into the caudal finfold at 7.0 to 7.2 mm. This pigment was associated with developing caudal rays in larger larvae. Pigment in the caudal fin increased rapidly when larvae exceeded 10.0 mm. Internal melanophores were first present in the hypural plate region on larvae 10.3 mm and longer. Larvae longer than 16.5 mm invariably had many melanophores among the rays of the caudal fin.

Transformation

Transformation of larvae to juveniles apparently was complete between 20 and 23 mm. Unfortunately, we preserved no specimens that were between 18.0 and 22.7 mm. However, our specimens of 17.8 and 18.0 mm were not completely transformed while the 22.7-mm specimen had acquired nearly all of the juvenile characteristics. Larvae began transforming at about 14.0 mm. At that time, proportional measurements relating preanal length, predorsal length, body depth, head length, snout length, and eye diameter to standard length (Table 4) began to change rapidly. Except for body depth, which continued to increase, the proportional measurements became nearly constant at 22.7 mm. The distribution of myomeres relative to other body parts became stable for specimens 22.7 to 36.2 mm (Table 3). Fin rays were completely ossified at 18.0 mm (Table 5), but the epural bones of the caudal skeleton were still unossified at that size. Although some scales were present on our 17.8- and 18.0-mm specimens, the 22.7-mm specimen was the smallest that was fully scaled. The slender, rodlike shape of the larva was replaced by the deeper bodied, laterally compressed form of the juvenile between 17.8 and 22.7 mm. The silvery coloration of juveniles was present on our specimens from 22.7 to 36.2 mm. Transformation included the following features: forward movement of the dorsal fin; shortening of the gut; forward movement of the anal fin; and relative increases in head length, snout length, eye diameter, and body depth. The same features were noted for transforming larvae of Atlantic thread herring (Richards et al. 1974) and scaled sardine (Houde et al. 1974).

COMPARISONS

Eggs and larvae of the genus *Brevoortia* almost always can be distinguished from those of other clupeid genera that spawn in marine waters of the south Florida and Gulf of Mexico region. Members of the genera *Alosa* and *Dorosoma* have demersal eggs, unlike those of *Brevoortia* which are pelagic. *Dorosoma* spawns in fresh waters and *Alosa* in fresh or nearly fresh waters, so that occurrence of their larvae with those of *Brevoortia* is unlikely. Larvae of *Alosa* spp. have more total myomeres than any species of *Brevoortia*, and the genera can be easily distinguished. Dwarf herrings (*Jenkinsia* spp.) might occur with *B. smithi* at the southern extreme of their range in Florida. Neither spawning habits nor eggs and larvae of *Jenkinsia* have been described, but the total myomeres of *Jenkinsia* did not exceed 42 (Miller and Jorgenson 1973), making it unlikely that larvae could be confused with *Brevoortia* which have higher myomere numbers (*Brevoortia*, 44-48). Since *B. smithi* may occur with either *B. tyrannus* or *B. patronus* and because hybrids are known (Dahlberg 1970), the specific identification of menhaden eggs and larvae from plankton collections is still in doubt where the species' ranges overlap.

Eggs of *B. smithi* are smaller than those of *Harengula jaguana* which range from 1.55 to 1.78 mm in diameter (Houde et al. 1974), and they cannot be confused with those of *Etrumeus teres* because eggs of that species have no oil globule. Our *B. smithi* eggs were similar to those of *Opisthonema oglinum* (Richards et al. 1974) and to

those of western Atlantic *Sardinella* sp. (Simpson and Gonzales 1967; Matsuura 1971; Houde and Fore 1973), but their average diameter was greater than for those species. Our *B. smithi* eggs ranged from 1.21 to 1.34 mm in diameter (mean = 1.27 mm) while those of *O. oglinum* are 1.10 to 1.28 mm (mean = 1.19 mm) (Richards et al. 1974) and those of western Atlantic *Sardinella* sp. are 1.00 to 1.32 mm (mean = 1.12-1.18 mm) (Simpson and Gonzales 1967; Matsuura 1971; Houde and Fore 1973). Reintjes (1962) reported *B. smithi* eggs ranging from 1.15 to 1.48 mm, including both planktonic and artificially fertilized eggs. The eggs of *O. oglinum* would not usually occur with those of *B. smithi* because *Opisthonema* spawns during spring and summer (Fuss et al 1969; Houde 1973a; Richards et al. 1974), while members of the genus *Brevoortia* are winter spawners (e.g., Turner 1969; Dahlberg 1970) in waters of south Florida and the Gulf of Mexico. *Sardinella* eggs could conceivably occur with those of *B. smithi*, but *Sardinella* probably spawns farther offshore than does *B. smithi*. Eggs of *B. tyrannus* apparently are larger than those of *B. smithi*, the reported diameters ranging from 1.30 to 1.95 mm (Mansueti and Hardy 1967). *Brevoortia patronus* eggs usually are slightly smaller than *B. smithi* eggs, the diameters ranging from 1.04 to 1.30 mm (Houde and Fore 1973). Hybrid embryos from artificial fertilization of *B. smithi* × *B. patronus* ranged from 1.05 to 1.18 mm (Hettler 1968).

Larvae of *Brevoortia* spp. have some distinctive characters that serve to distinguish them from other clupeid larvae with which they may occur. Newly hatched larvae of *B. smithi* have been photographed by Reintjes (1962), but these photographs fail to show distinguishing characters of larvae in that size range. Hettler (1970a) presented illustrations of 7.6- and 11.9-mm TL larvae of *B. smithi*, but only the 11.9-mm specimen has some characteristics illustrated that help to identify it as a *Brevoortia* sp.

Myomere numbers ranged from 45 to 47 in *B. smithi*, thus separating it from *H. jaguana* (42 or fewer) (Houde et al. 1974) and *E. teres* (48 or more) (Houde and Fore 1973). Total myomere counts of *B. smithi* overlap those of *O. oglinum* (45 to 49), *Sardinella* sp. (45 to 47) (Houde and Fore 1973), and the other species of *Brevoortia*. Numbers of postdorsal-preanus myomeres always were fewer than 5 in *B. smithi* larvae longer than 10 mm and never exceeded 6 in smaller larvae (usually 4 or 5). The other identified clupeid genera from this region, excepting *Etrumeus*, have 5 or more (usually 6 to 9) postdorsal-preanus myomeres in all length classes, thus serving to distinguish them from *Brevoortia* larvae.

Pigmentation of newly hatched *Brevoortia* larvae apparently differs from that of other clupeid genera in its details. Recently hatched *B. smithi* larvae have pigment on both the dorsal and ventral sides of the notochord tip (Figures 2A-3B), distinguishing them from other co-occurring clupeid genera, except for some specimens of *Harengula* (see Houde et al. 1974). *Brevoortia tyrannus* has pigmentation similar to *B. smithi* at the notochord tip (Mansueti and Hardy 1967), and we suspect that *B. patronus* also has this pigment characteristic based on our observations of *Brevoortia* larvae that were collected in the northern Gulf of Mexico, where *B. patronus* is known to spawn. Recently hatched larvae of *O. oglinum*, *Sardinella* sp., and *E. teres* have pigment only on the ventral side of the notochord tip.

Lateral pigmentation is present on *B. smithi* larvae as small as 5.2 mm—which is smaller than other clupeids found in their geographical range. At 10 to 12 mm, most of our *B. smithi* larvae had more than 5 melanophores on their sides, and some had as many as 25. No larvae of *Harengula*, *Opisthonema*, *Sardinella*, or *Etrumeus* that we have observed have had pigment on the sides until they were at least 15 mm in length. We do not know if *B. tyrannus* or *B. patronus* develop lateral pigmentation at sizes as small as *B. smithi*, but illustrations of *B. tyrannus* larvae (Mansueti and Hardy 1967) from 8 to 23 mm do not show any such pigment, nor is it mentioned in their text.

Size at transformation varies among clupeid species. *Brevoortia smithi* had completed transformation at about the same size as *H. jaguana* (Houde et al. 1974) and *O. oglinum* (Richards et al. 1974), at lengths from 20 to 24 mm. However, other species of *Brevoortia* apparently do not transform until they are of larger size. *Brevoortia tyrannus* exceeds 30 mm before having a typical juvenile form (Mansueti and Hardy 1967), and the observations and morphological data of Suttkus (1956) suggest that *B. patronus* does not transform until 28 mm or longer. It is possible that our tank-reared *B. smithi* transformed at smaller sizes than in nature, but the seemingly good growth rate and the selection of normal appearing larvae to describe development lead us to believe that *B. smithi* is transformed at approximately 22 mm.

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LITERATURE CITED

AHLSTROM, E. H.
1968. Book review of: Mansueti, A. J., and J. D. Hardy, Jr. 1967. Development of fishes of the Chesapeake Bay region, an atlas of egg, larval, and juvenile stages, Part I. Copeia 1968:648-651.

DAHLBERG, M. D.
1970. Atlantic and Gulf of Mexico menhadens, genus *Brevoortia* (Pisces: Clupeidae). Bull. Fla. State Mus. Biol. Sci. 15:91-162.

DECIECHOMSKI, J. D.
1968. Huevas y larvas de tres especies de peces marinos, *Anchoa marinii*, *Brevoortia aurea* y *Prionotus nudigula* de la zona de Mar del Plata. Bol. Inst. Biol. Mar. Mar del Plata 17:1-28.

FUSS, C. M., JR., J. A. KELLY, JR., AND K. W. PREST, JR.
1969. Gulf thread herring; aspects of the developing fishery and biological research. Proc. Gulf Caribb. Fish. Inst., 21st Annu. Sess., p. 111-125.

HETTLER, W. F., JR.
1968. Artificial fertilization among yellowfin and Gulf menhaden (*Brevoortia*) and their hybrid. Trans. Am. Fish. Soc. 97:119-123.
1970a. Rearing larvae of yellowfin menhaden, *Brevoortia smithi*. Copeia 1970:775-776.
1970b. Rearing menhaden. *In* Research in fiscal year 1969 at the Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C., p. 24-26. U.S. Fish Wildl. Serv., Circ. 350.

HILDEBRAND, S. F.
1963. *Family* Clupeidae. *In* Fishes of the western North Atlantic. Part Three, p. 257-454. Mem. Sears Found. Mar. Res., Yale Univ. 1.

HOUDE, E. D.
1973a. Estimating abundance of sardine-like fishes from egg and larval surveys, Eastern Gulf of Mexico: preliminary report. Proc. Gulf Caribb. Fish. Inst., 25th Annu. Sess., p. 68-78.
1973b. Some recent advances and unsolved problems in the culture of marine fish larvae. Proc. World Mariculture Soc. 3:83-112.

HOUDE, E. D., AND P. L. FORE.
1973. Guide to identity of eggs and larvae of some Gulf of Mexico clupeid fishes. Fla. Dep. Nat. Resour., Mar. Res. Lab., Leafl. Ser. 4, Part 1, No. 23, 14 p.

HOUDE, E. D., AND B. J. PALKO.
1970. Laboratory rearing of the clupeid fish *Harengula pensacolae* from fertilized eggs. Mar. Biol. (Berl.) 5:354-358.

HOUDE, E. D., W. J. RICHARDS, AND V. P. SAKSENA.
1974. Description of eggs and larvae of scaled sardine, *Harengula jaguana*. Fish. Bull., U.S. 72:1106-1122.

LEVI, E. J.
1973. Juvenile yellowfin menhaden from the Bahama Islands. Trans. Am. Fish. Soc. 102:848-849.

MANSUETI, A. J., AND J. D. HARDY, JR.
1967. Development of fishes of the Chesapeake Bay region. An atlas of egg, larval and juvenile stages. Part I. Nat. Resour. Inst., Univ. Md., 202 p.

MATSUURA, Y.
1971. A study of the life history of Brazilian sardines, *Sardinella aurita*. I. Distribution and abundance of sardine eggs in the region of Ilha Grande, Rio de Janeiro. Bol. Inst. Oceanogr. (Sao Paulo) 20:33-60.

MILLER, G. L., AND S. C. JORGENSON.
1973. Meristic characters of some marine fishes of the western Atlantic Ocean. Fish Bull., U.S. 71:301-312.

REINTJES, J. W.
1962. Development of eggs and yolk-sac larvae of yellowfin menhaden. U.S. Fish Wildl. Serv., Fish. Bull. 62:93-102.

RICHARDS, W. J., R. V. MILLER, AND E. D. HOUDE.
1974. Egg and larval development of the Atlantic thread herring, *Opisthonema oglinum*. Fish. Bull., U.S. 72:1123-1136.

SIMPSON, J. G., AND G. GONZALEZ.
1967. Some aspects of the early life history and environment of the sardine, *Sardinella anchovia*, in eastern Venezuela. Ser. Recursos Explor. Pesq. 1:38-93.

SUTTKUS, R. D.
1956. Early life history of the largescale menhaden, *Brevoortia patronus*, in Louisiana. Trans. North Am. Wildl. Conf. 21:390-407.

TAYLOR, W. R.
1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus. 122(3596):1-17.

TURNER, W. R.
1969. Life history of menhadens in the eastern Gulf of Mexico. Trans. Am. Fish. Soc. 98:216-224.

NOTES

TWO BLOOMS OF *GYMNODINIUM SPLENDENS*, AN UNARMORED DINOFLAGELLATE

Little is known about the ecology and physiology of an unarmored dinoflagellate (30 to 50 μm), *Gymnodinium splendens* Lebour, although feeding experiments have shown it to be an important food source for certain marine herbivores. Lasker et al. (1970) found that anchovy larvae may be reared the first week upon unialgal suspensions of *G. splendens* while Paffenhöfer (1970, 1971) and Barnett (1974) showed it to be a preferred food for *Calanus finmarchicus* and larval stages of *Labidocera trispinosa*. Pokorny and Gold (1973) reported on cell ultrastructure of *G. splendens*, Sweeney (1954) observed vitamin B_{12} requirements, and Thomas et al. (1973) described optimal light and temperature requirements. In addition to these laboratory studies, Loftus et al. (1972) have noted *G. splendens* in a bloom of diverse dinoflagellate species in Chesapeake Bay.

This note reports upon two field studies of blooms of *G. splendens*. The first observation was made in Coyote Bay of Bahia Concepción, Gulf of California, where *G. splendens* was the dominant phytoplankter in March 1971. The second observation was made in March 1974, when large concentrations were observed in coastal waters of the Southern California Bight. In both occurrences *G. splendens* dominated the phytoplankton crop so that measurements of primary production and the chemical composition of suspended particles allowed a reasonable description of this species.

Gymnodinium splendens in Coyote Bay

Coyote Bay (lat. 26°43.0′N, long. 111°53.0′W) of Bahia Concepción is well protected and shallow. Chemical and physical observations were made while the ship (RV *E. B. Scripps*) was at anchor in 20 m of water and included measurements of particulate adenosine triphosphate (Holm-Hansen and Booth 1966) and chlorophyll (Yentsch and Menzel 1963; Holm-Hansen et al. 1965), microscopic examination of water samples preserved in 5% (V/V) buffered Formalin[1] (Utermöhl 1958), and determinations of primary production based upon rates of incorporation of radioactive carbon (Steemann Nielsen 1952). The depth distribution of phytoplankton was recorded at regular intervals by continuous vertical profiles to the bottom with both a submersible transmissometer (Petzold and Austin 1968) and a fluorometer attached to a hose and submersible pump (Lorenzen 1966; Kiefer and Austin 1974). The continuous profiles of in situ fluorescence were translated into chlorophyll *a* concentrations by frequent calibration with discrete samples which were analyzed fluorometrically for chlorophyll and phaeophytin concentration (Kiefer 1973).

The five phytoplankters which occurred together and were numerically most abundant in Coyote Bay were: *G. splendens* (1.0×10^5/liter), *Leptocylindrus danicus* (3.4×10^4/liter), *Skeletonema costatum* (1.4×10^3/liter), *Cerataulina bergonii* (1.4×10^3/liter), and *Thalassiothrix frauenfeldii* (4.0×10^3/liter). Chlorophyll concentration varied with depth and ranged from 4.4 μg/liter to 13 μg/liter for numerous samplings of the 20-m water column. Figure 1 shows a time sequence of profiles of in situ fluorescence of chlorophyll. Profiles of light transmission displayed a similar stratified structure. The increase in depth of the upper chlorophyll maximum between 1845 and 2300 and the decrease in depth between 2300 and 0720 the following day indicated a diel migration of *G. splendens*. This suggestion was supported by the predominance of *G. splendens* in the maxima and by the improbability of physical factors such as advection or internal waves affecting such variations. Conditions were calm at the sea surface and the water column was isothermal with depth.

The upper chlorophyll maximum (Figure 1) moved downward at sunset with a velocity of approximately 1.7 m/h. Such velocities are similar to those of other dinoflagellates. For example, a natural bloom of *Ceratium furca* occurring off the southern California coast was observed to migrate downward at 2 m/h and mass cultures of *Cachonina niei* and *Gonyaulax polyedra* displayed migratory rates of 1 to 2 m/h (Eppley et al. 1968). Our observations suggested that a portion of the *G. splendens* population moved upward between 2300 and 0400 the following day. Since sunrise was

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

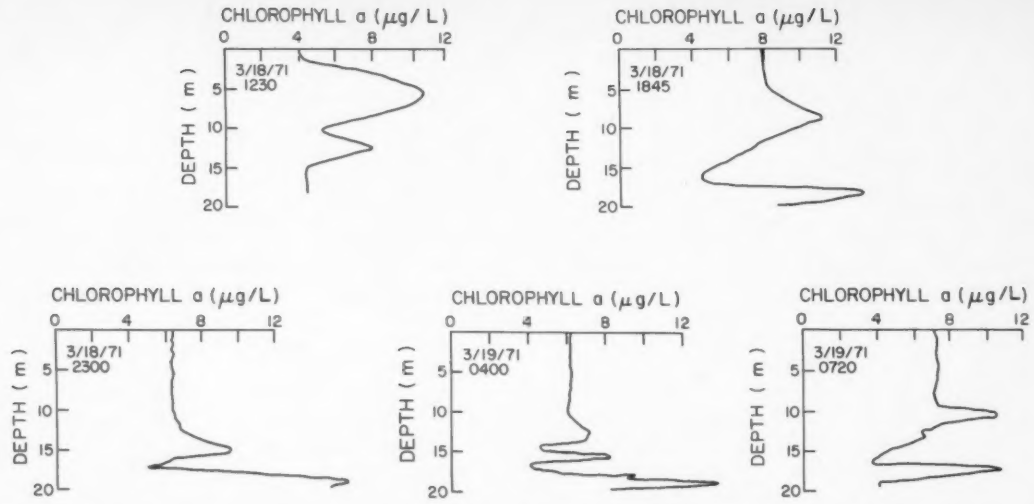

FIGURE 1.—Profiles of the concentration of chlorophyll *a* based upon fluorescence profiles. The upper layer of *Gymnodinium splendens* at 1230 h was concentrated at 6 m; by 1845 it had moved to 8 m and reached 15 m by 2300. Movement upward commenced at 0200 reaching 10 m by 0720. The lower layer remained relatively close to the bottom during this time.

around 0600, this movement may originate from a biological clock rather than from a phototactic response. These observations partially conflict with laboratory studies of phototaxis in *G. splendens* (Forward 1974). He found that not only was the cell strongly phototactic but that the strength of the response was subject to a circadian rhythm, being strongest at the end of the entrained dark period.

By assuming that *G. splendens* dominated the production as well as the standing crop of phytoplankton in Coyote Bay, we obtain information on the steady state doubling time for the species. Water samples were collected from four depths, 0, 5, 10, and 18 m, inoculated with $NaH^{14}CO_3$, and incubated from sunrise to sunset in situ. Primary production was then determined from rates of light-induced incorporation of ^{14}C into particles removed by filtration. The water samples were also analyzed for concentrations of chlorophyll *a* and adenosine triphosphate (ATP). By multiplying the concentration of ATP by 250, we obtained an estimate of "living-carbon" (Holm-Hansen and Booth 1966); this estimate allowed a crude determination of doubling time t_d from the steady-state equation:

$$t_d = \frac{\ln 2}{\mu} = \frac{C \cdot \ln 2}{\Delta C/\Delta t}$$

where μ is the specific growth rate and equal to the rate of carbon assimilation, $\Delta C/\Delta t$, divided by C, the concentration of cell carbon. On this basis, the doubling time for *G. splendens* at 0, 5, 10, and 18 m was 2.3, 2.6, 2.7, and 62 days, respectively (Table 1). These estimates of doubling time for a natural population of *G. splendens* may be compared with a maximal doubling time of 1.6 days for cells grown in the laboratory (Thomas et al. 1973). We also note that our estimates of the chlorophyll *a* concentration per cell yielded a value of approximately 100 pg/cell, typical for laboratory cultures (Bailey 1974).

TABLE 1.—Production, chlorophyll *a*, ATP, and doubling time for a *Gymnodinium splendens* bloom in Coyote Bay, Gulf of California.

Depth (m)	Production (μg C/liter•day)	Chlorophyll *a* concentration (μg/liter)	ATP (μg/liter)	Doubling time (days)
0	125	5.8	1.7	2.3
5	108	5.3	1.6	2.6
10	126	6.2	1.9	2.6
18	35	4.7	1.3	62

Gymnodinium splendens in the Southern California Bight

A second bloom of *G. splendens* was observed in March 1974, along the southern coast of California,

during a cruise on RV *David Starr Jordan*. Stations in the sampling program extended along the 20-fathom contour from Malibu (lat. 34°00.8′N, long. 118°40.6′W) south to San Onofre (lat. 32°56.0′N, long. 117°17.4′W). Intermediate stations included Manhattan Beach (lat. 33°52.5′N, long. 118°27.0′W), Seal Beach (lat. 33°36.5′N, long. 119°04.3′W), and Dana Point (lat. 33°26.3′N, long. 117°42.8′W). A sixth station was on the 270-fathom contour off Laguna Beach (lat. 33°30.8′N, long. 117°50.3′W).

Continuous vertical profiles of in situ chlorophyll fluorescence were made to a depth of 35 m. Water from the outflow of the fluorometer was collected at the surface and within the fluorescence maximum. Three analyses were made on subsamples of water from the two depths. First, the size distribution of suspended particles was immediately determined with an electronic particle counter (model T_a Coulter Counter). We accumulated counts in the upper nine channels which gave us a frequency distribution for particles with equivalent diameters ranging from 20 to 128 μm. Second, subsamples were preserved in 5% Formalin for species determination. Third, the chlorophyll *a* concentration in each subsample was determined fluorometrically for acetone extracts of filtered particles.

Vertical profiles made at various times of the day and night at each of the six stations on the 20-fathom contour were characterized by a unimodal distribution of chlorophyll. The chlorophyll maximum varied little in depth from 15 to 20 m within a moderately developed thermocline, and was most often less than 4 m thick. At these stations, *G. splendens* contributed most of the phytoplankton crop within the maxima. However, in surface waters it contributed a much smaller fraction of the crop. The highest concentration (Figure 2) of *G. splendens* was within the well-defined maximum at Seal Beach where its concentration reached 4×10^5 cells/liter (chlorophyll a = 42.0 μg/liter). The lowest concentration within a maximum was at Manhattan Beach, 1.2×10^4 cells/liter (chlorophyll a = 1.3 μg/liter.

The predominance of *G. splendens* in the chlorophyll maximum was also evident from the particle size distributions obtained with the electronic particle counter. Within the maximum, particles with equivalent diameters between 36 and 57 μm far outnumbered smaller- and larger-sized particles. In surface waters the smaller-sized

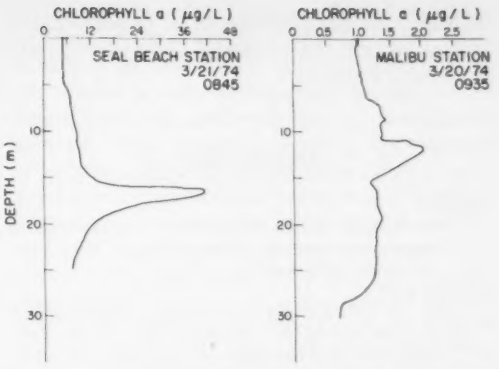

FIGURE 2.—Profiles of the concentration of chlorophyll *a* based upon fluorescence profiles at two stations along the 20-fathom contour of the Southern California Bight. The subsurface maxima are predominantly composed of *Gymnodinium splendens*.

particles outnumbered particles of the size of *G. splendens*. The other phytoplankton in surface waters included *Ceratium furca* and *C. kofoidii*, *Dinophysis acuminata*, and a species of *Gyrodinium*. Very few diatoms were present.

It appeared that the bloom of *G. splendens* dissipated seaward since the subsurface chlorophyll maximum was poorly developed at the Laguna Beach station which was on the 270-fathom contour. Here the concentration of chlorophyll in the maximum was only 0.76 μg/liter, while the concentration at the surface was 0.63 μg/liter. In addition, both the particle size distribution and microscopic counts indicated a more diverse assemblage of dinoflagellate species at this station, with the unarmored dinoflagellate *Cochlodinium catenatum* being most abundant.

Thus, the bloom of *G. splendens* appeared to be limited to nearshore waters, in a band extending as far as 100 km along the coast. This subsurface bloom was presumed to be a large food source for planktonic herbivores, but more field sampling is necessary to determine whether the bloom is a seasonal occurrence. In another paper, Lasker (1975) describes the feeding responses of anchovy larvae to these natural concentrations of *G. splendens*.

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Literature Cited

BAILEY, T.
1974. Chemical responses of two marine dinoflagellates to nitrate and phosphate limitation. M. A. Thesis, Univ. California, Santa Barbara.

BARNETT, A. M.
1974. The feeding ecology of an omnivorous neritic copepod, *Labidocera trispinosa* (Esterly). Ph.D. Thesis, Univ. California, San Diego, 215 p.

EPPLEY, R. W., O. HOLM-HANSEN, AND J. D. H. STRICKLAND.
1968. Some observations on the vertical migration of dinoflagellates. J. Phycol. 4:333-340.

FORWARD, R. B., JR.
1974. Phototaxis by the dinoflagellate *Gymnodinium splendens* Lebour. J. Protozool. 21:312-315.

HOLM-HANSEN, O., AND C. R. BOOTH.
1966. The measurement of adenosine triphosphate in the ocean and its ecological significance. Limnol. Oceanogr. 11:510-519.

HOLM-HANSEN, O., C.J. LORENZEN, R.W. HOLMES, AND J. D. H. STRICKLAND.
1965. Fluorometric determination of chlorophyll. J. Cons. 30:3-15.

KIEFER, D. A.
1973. Fluorescence properties of natural phytoplankton populations. Mar. Biol. (Berl.) 22:263-269.

KIEFER, D. A., AND R. W. AUSTIN.
1974. The effect of varying phytoplankton concentration on submarine light transmission in the Gulf of California. Limnol. Oceanogr. 19:55-64.

LASKER, R.
1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453-462.

LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.
1970. Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5:345-353.

LOFTUS, M. E., D. V. SUBBA RAO, AND H. H. SELIGER.
1972. Growth and dissipation of phytoplankton in Chesapeake Bay. I. Response to a large pulse of rainfall. Chesapeake Sci. 13:282-299.

LORENZEN, C. J.
1966. A method for the continuous measurement of *in vivo* chlorophyll concentration. Deep-Sea Res. 13:223-227.

PAFFENHÖFER, G.-A.
1970. Cultivation of *Calanus helgolandicus* under controlled conditions. Helgoländer wiss. Meeresunters. 20:346-359.
1971. Grazing and ingestion rates of nauplii, copepodids and adults of the marine planktonic copepod *Calanus helgolandicus*. Mar. Biol. (Berl.) 11:286-298.

PETZOLD, T. J., AND R. W. AUSTIN.
1968. An underwater transmissometer for ocean survey work. Scripps Inst. Oceanogr. Ref. 68-59, 5 p.

POKORNY, K. S., AND K. GOLD.
1973. The morphological types of particulate inclusions in marine dinoflagellates. J. Phycol. 9:218-224.

STEEMANN NIELSEN, E.
1952. The use of radio-active carbon (C^{14}) for measuring organic production in the sea. J. Cons. 18:117-140.

SWEENEY, B. M.
1954. Gymnodinium splendens, a marine dinoflagellate requiring vitamin B_{12}. Am. J. Bot. 41:821-824.

THOMAS, W. H., A. N. DODSON, AND C. A. LINDEN.
1973. Optimum light and temperature requirements for *Gymnodinium splendens*, a larval fish food organism. Fish. Bull., U.S. 71:599-601.

UTERMÖHL, H.
1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. Int. Ver. Theor. Angew. Limnol. Verh. 17:47-71.

YENTSCH, C. S., AND D. W. MENZEL.
1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. Deep-Sea Res. 10:221-231.

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ENHANCED SURVIVAL OF LARVAL GRASS SHRIMP IN DILUTE SOLUTIONS OF THE SYNTHETIC POLYMER, POLYETHYLENE OXIDE[1]

Small amounts of linear, high molecular weight synthetic polymers when added to liquids can significantly reduce frictional resistance in turbulent pipe and channel flow (Castro and Squire 1967; Peterson et al. 1974). These drag-reducing agents have potential for improving efficiency of sewer, water, and fire-fighting systems (Castro 1972); reducing friction around ships' hulls (Wade 1973); and perhaps increasing water flow and circulation in mariculture operations (Zielinski et al. in press). Such uses may result in the introduction of relatively large quantities of polymers into nearshore marine and estuarine waters or culture tanks.

We report here experiments to evaluate effects of chronic exposure to polyethylene oxide, a very effective friction-reducing additive, on larvae of estuarine grass shrimp, *Palaemonetes vulgaris* and *P. pugio*. This polymer exhibits a very low

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degree of toxicity and is approved for food contact applications and as an additive to some foods (Smyth et al. 1970). *Palaemonetes* shrimp were chosen for this study because of their importance in estuarine food chains (Hedgpeth 1947; Welsh 1973), the ease with which their larvae may be cultured in the laboratory, the general similarity of their larvae to those of *Macrobrachium* shrimp being evaluated for commercial culture, and the known sensitivity of these carideans to a variety of toxic agents (Lowe et al. 1971; Hansen et al. 1973; Redmann 1973; Sandifer and Shealy 1974[2]).

Methods and Materials

Two experiments were conducted with *P. vulgaris*, one with *P. pugio*. Effects of three polyethylene oxide concentrations (25, 50, and 100 wppm—weight parts per million) were tested versus controls in all experiments. Forty *Palaemonetes vulgaris* larvae were reared at each condition in experiments I (10 replicates of 4 animals each in 10.5-cm finger bowls) and II (4 replicates of 10 animals each in 19.1-cm bowls), while 72 *P. pugio* zoeae (4 replicates of 18 each) were maintained at each concentration in experiment III. The *P. pugio* larvae were isolated in compartments of covered plastic boxes. The culture containers were placed in a Percival Model I-35VL incubator[3] (Percival Manufacturing Co., Boone, Iowa) where temperature was held at approximately 25°C in experiment I and 28°C in the subsequent trials. A 14-h light – 10-h dark schedule was maintained in all studies. All animals were transferred to clean containers with fresh, filtered seawater (30‰ salinity) and fed newly hatched nauplii of *Artemia salina* daily.

Fresh stock solutions (200 wppm) of polyethylene oxide (Polyox Coagulant, molecular weight approximately 5×10^6 [Union Carbide Corp.]) in seawater were prepared every 3 or 4 days. Test solutions were prepared by diluting the stock with appropriate volumes of seawater.

Results and Discussion

Addition of small amounts of polyethylene oxide to the culture water significantly enhanced the survival of grass shrimp larvae in static water culture (Figure 1). The polymer affected neither the number of molts to the postlarval stage nor the size of postlarvae produced. However, a slight but definite trend toward increasing development time with increasing polyethylene oxide concentration was apparent in all experiments (Table 1).

Stranding of larvae above the waterline on the walls of the culture containers was a significant cause of mortality in all control cultures, but addition of ≥25-wppm polyethylene oxide virtually eliminated stranding deaths (Figure 1). This effect was probably the result of the reduced surface tension and increased viscosity, lubricity, and stringiness of the treatment solutions. Of course, this type of effect would not be manifested in

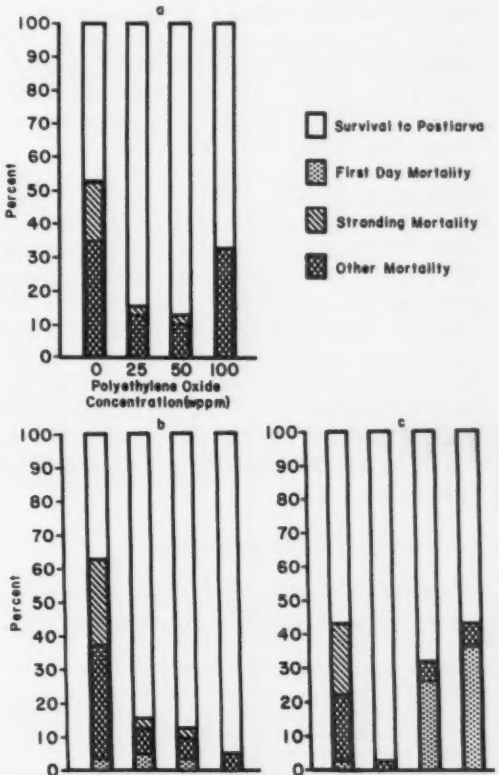

FIGURE 1.—Percentage survival and mortality of *Palaemonetes* larvae reared in polymer and control solutions. (a) *P. vulgaris* experiment I, (b) *P. vulgaris* experiment II, (c) *P. pugio*.

[2]Sandifer, P. A., and M. H. Shealy, Jr. 1974. Some effects of mercury on survival and development of larval grass shrimp, *Palaemonetes vulgaris* (Say). (Unpubl. manuscr.)

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA; NOAA Office of Sea Grant; or the State of South Carolina.

TABLE 1.–Development of *Palaemonetes* larvae exposed to polyethylene oxide solutions (Mean with standard deviation).

Experiment	Species	Polyethylene oxide concentration (wppm) 0	25	50	100
		Development time (days)			
I	*Palaemonetes vulgaris*	19.1 ± 1.5	20.9 ± 2.0	21.3 ± 2.5	22.1 ± 2.8
II	*P. vulgaris*	14.3 ± 0.9	14.6 ± 0.8	14.9 ± 0.9	15.6 ± 1.4
III	*P. pugio*	15.5 ± 1.6	15.5 ± 1.5	16.2 ± 1.4	16.2 ± 2.1
		Molts to postlarva			
III	*P. pugio*	8.0 ± 0.8	8.1 ± 0.9	8.5 ± 0.8	8.3 ± 1.4
		Length of postlarvae (mm)			
II	*P. vulgaris*	6.5 ± 0.6	6.4 ± 0.5	6.4 ± 0.5	6.1 ± 0.5
III	*P. pugio*	6.6 ± 0.6	6.6 ± 0.6	6.6 ± 0.6	6.6 ± 0.5

natural waters, but it may appear in tank culture operations.

First-day mortalities were significant only in the higher treatment concentrations when *P. pugio* larvae were reared in covered plastic boxes (Figure 1c). These deaths apparently were the result of oxygen depletion in the culture water caused by overfeeding and the relatively high biochemical oxygen demand of the polymer solutions (Wade 1973). Other mortalities totaled only 5.6 and 6.9% in the 50- and 100-wppm concentrations, respectively, after the first day.

In all but one instance, larvae in the polymer solutions exhibited a marked reduction in other mortalities (i.e., "natural" deaths) over the controls. Thus, in addition to eliminating stranding, the polyethylene oxide somehow acted to reduce other causes of mortality. The reason for this beneficial effect is unknown, but it is unlikely to be nutritional since, in vertebrates at least, the polymer is poorly absorbed from the gut (Smyth et al. 1970). Further study is needed to examine the reasons for this effect and to evaluate the potential of polyethylene oxide for use in mariculture operations.

Acknowledgments

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Literature Cited

CASTRO, W. E.
1972. Reduction of flow friction with polymer additives. Water Resour. Res. Inst., Clemson Univ., Rep. 24:1-56.

CASTRO, W. E., AND W. SQUIRE.
1967. The effect of polymer additives on transition in pipe flow. Appl. Sci. Res. 18:81-96.

HANSEN, D. J., S. C. SCHIMMEL, AND J. M. KELTNER, JR.
1973. Avoidance of pesticides by grass shrimp (*Palaemonetes pugio*). Bull. Environ. Contam. Toxicol. 9:129-133.

HEDGPETH, J. W.
1947. River shrimps, interesting crustaceans about which little has been written. Prog. Fish-Cult. 9:181-184.

LOWE, J. I., P. R. PARRISH, A. J. WILSON, JR., P. D. WILSON, AND T. W. DUKE.
1971. Effects of mirex on selected estuarine organisms. Trans. 36th North Am. Wildl. Nat. Resour. Conf., p. 171-186.

PETERSON, J. P., W. E. CASTRO, P. B. ZIELINSKI, AND W. F. BECKWITH.
1974. Increased turbulent dispersion in high polymer drag reducing open channel flow. ASCE (Am. Soc. Civ. Eng.) Proc., Hydraul. Div. Hy6:773-785.

REDMANN, G.
1973. Studies on the toxicity of mirex to the estuarine grass shrimp, *Palaemonetes pugio*. Gulf Res. Rep. 4:272-277.

SMYTH, H. F., JR., C. S. WEIL, M. D. WOODSIDE, J. H. KNAAK, L. J. SULLIVAN, AND C. P. CARPENTER.
1970. Experimental toxicity of a high molecular weight poly (ethylene oxide). Toxicol. Appl. Pharmacol. 16:442-445.

WADE, R. H.
1973. The pollution potential of drag reducing polymers. *In* N. D. Sylvester (editor), Drag reduction in polymer solutions, p. 87-90 Am. Inst. Chem. Eng., N.Y.

WELSH, B. L.
1973. The grass shrimp, *Palaemonetes pugio*, as a major component of a salt marsh ecosystem. Ph.D. Thesis, Univ. Rhode Island, Kingston, 90 p.

ZIELINSKI, P. B., W. E. CASTRO, AND P. A. SANDIFER.
In press. The evaluation and optimization of *Macrobrachium* shrimp larva tank designs and support systems. Proc. World Mariculture Soc. 5.

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A COMPUTER PROGRAM FOR ANALYSIS OF POLYMODAL FREQUENCY DISTRIBUTIONS (ENORMSEP), FORTRAN IV

Program ENORMSEP (Extended Normal Separator Program) separates a polymodal frequency distribution into its component groups where aging studies have not been or cannot be performed. The program calculates preliminary estimates of the number of size groups and their points of overlap using probit analysis and polynomial regression techniques. These preliminary estimates are then entered into NORMSEP (Normal Separator Program) (Hasselblad 1966), used as a subroutine, in order to complete the analysis.

Output data are generated both as listings and punched cards. Listings include at the option of the user: 1) table of values of the standardized normal distribution; 2) table of values of probabilities, standardized normal variables, and probits; 3) polynomial regressions and analyses of variance of probits; 4) table of residuals for the final regression; 5) table of roots corresponding to all regressions after taking second derivative; 6) tables for analyses for the separation of modes; 7) plots of observed and predicted values for the final regression; and 8) plot of the original frequency distribution. Punched card output includes the number of observed frequency distributions with their intervals and probits and regression coefficients for the polynomials.

Input data require the observed size frequency together with values for identification and control purposes. No more than nine size groups may be separated because of limits on the efficiency of parameter estimate in the polynomial regression.

This computer program was developed on an IBM 360/65I computer[1] using release 20.7 MVT/HASP system at the Statistical and Computing Center at the University of Hawaii. This computer program is capable of processing multiple sets of data. For a "typical" problem, the program takes about 1 min of central processing unit time and a total machine unit time of 1.5 min to run a single problem "individually." The requirement for core storage is 168K, where K is 1,024 bytes and where a byte is an address collection consisting of eight binary bits or binary digits.

A description of the program, including program listing as well as input and output for two examples, is available from the authors upon request.

[1]Reference to this particular computer system does not imply endorsement of the product by the National Marine Fisheries Service, NOAA, but is given to provide the reader with a base for determining the cost of performing jobs with the particular computer system at his disposal.

Literature Cited

HASSELBLAD, V.
1966. Estimation of parameters for a mixture of normal distributions. Technometrics 8:431-444.

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RECORDS OF LARVAL, TRANSFORMING, AND ADULT SPECIMENS OF THE QUILLFISH, *PTILICHTHYS GOODEI*, FROM WATERS OFF OREGON

This report extends the southern range of the quillfish, *Ptilichthys goodei* Bean 1881, in the northeast Pacific to waters off the central coast of Oregon where larval, transforming, and adult specimens have been collected. The previously reported range of this species in the North Pacific was from the Okhotsk and Bering seas to northern Washington and Puget Sound (DeLacy et al. 1972; Quast and Hall 1972; Hart 1973). The life history of the quillfish is poorly understood and nothing is known of the early stages (Walker 1953; Makushok 1958; Grinols 1965; Hart 1973).

Materials and Methods

Three larvae (20.3, 24.7, 36.0 mm SL—standard length) and one transforming specimen (114 mm SL) of *P. goodei* came from plankton collections made with large-mouth (0.7 m) bongos having 0.571-mm mesh nets. Tows were made in a step-oblique or oblique manner from near the bottom or 150 m (at deeper stations) to the surface at a vessel speed of 2 knots. Tow times were 16 to 25 min. The specimens were fixed in 10% and stored in 5% buffered Formalin.[1]

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Two adults (272, 309 mm SL) of *P. goodei* came from otter trawl (5-m headrope, 4-cm stretch mesh body, 1.25-cm mesh cod end liner) collections. The trawl was towed on the bottom for 15 min at a speed of 2 to 3 knots. The specimens were fixed in 10% Formalin and stored in 40% isopropyl alcohol.

Body measurements were made as described by Hubbs and Lagler (1958). For larvae, standard length was measured from snout tip to notochord tip. The point of reference used to determine notochord tip in larvae of *P. goodei* is indicated by an arrow in Figure 1. It is the point near the end of the tail, at the posterior edge of the region having no pigment on the ventral margin. This point was determined from the tail tip of the 114-mm specimen which had been stained with alizarin red S.

Meristic counts were made on unstained larval and transforming specimens and radiographs of the adults.

Results

Descriptions

The larvae of *P. goodei* are characterized by their slender, elongate form; gut length (35-40% SL, decreasing with growth); myomere numbers, (55 to 57) + (170 to 174) = 225 to 229; and pigment pattern (Figure 1). Morphometrics and meristics are in Table 1. Compared with adults, the larvae have a short snout (17-18% HL—head length) and no fleshy protrusion of the lower jaw. The mouth is oblique. Dorsal and anal fin rays are evident in the 36-mm specimen but the adult numbers have not been attained. The spines of the first dorsal and the rays of the second dorsal begin to form at the posterior and anterior ends of the fins respectively. Development then proceeds anteriorly in the first dorsal fin and posteriorly in the second dorsal. The anal fin rays begin to form slightly anterior to the center of the fin with development proceeding anteriorly and posteriorly. Pectoral fin rays were not formed and pelvic fins were absent in the size range examined.

Pigmentation (Figure 1) on the three larval specimens is similar. Head pigmentation consists of that on the lower jaw, anterior part of the upper jaw, throat, and internally at the base of the hindbrain. Gut pigmentation is mostly restricted to the dorsal and ventral surface with some additional melanophores scattered over the anterior region. The melanophores on the ventral gut sur-

FIGURE 1.—Larva of *Ptilichthys goodei* from waters off Oregon (arrow indicates point of reference for SL).

TABLE 1.—Morphometrics (mm) and meristics of *Ptilichthys goodei* from Oregon waters.

Morphometrics										Meristics								
													P_1			Myomeres		
SL	TL[1]	Snout length	Eye diameter	Head length	Upper jaw length	Lower jaw length	Snout to anus	Depth at pectoral base	Depth at anus	DI	DII[2]	A[2]	Left	Right	Branchiostegals	Preanal	Postanal	Total
Larvae:																		
20.3	21.0	0.4	0.7	2.3	0.8	1.1	8.0	0.9	0.9	—	—	—	—	—	—	55	174	229
24.7	25.5	0.4	0.6	2.2	0.7	1.1	9.3	1.1	1.1	—	—	—	—	—	—	55	170	225
36.0	36.9	0.5	0.7	2.7	0.9	1.1	12.5	1.1	1.1	40	~80	~113	—	—	5	57	170	227
Transforming:																		
114	117	1.6	1.1	6.1	1.8	2.6	32.2	2.0	2.0	83	148	179	13	13	5	55	172	227
																Vertebrae		
Adults:																Abdominal	Caudal[3]	Total
272	276	5.2	2.8	17.0	3.8	5.0	81	5.5	7.0	83	144	180	13	13	5	53	174	227
309	313	6.3	3.0	19.0	4.2	6.0	91	6.0	7.7	88	142	181	13	13	5	53	174	227

[1]Total length is given for comparison with other publications, although the long caudal filament was not intact.
[2]Dorsal and anal fin ray counts include possible caudal fin elements dorsal and ventral to the fleshy caudal extension respectively.
[3]One fused caudal vertebra found in each adult specimen was counted as one vertebra.

face form a single row on the anterior one-fourth to one-half the length of the gut and a double row along the remaining length. Body pigmentation is concentrated dorsally and ventrally. From a dorsal view, the dorsal melanophores appear somewhat as a double row, one on each side of the dorsal midline, extending from a point over the middle of the gut to near the tail tip (arrow in Figure 1). These dorsal melanophores are larger than the ventral ones. Ventrally, a heavy concentration of melanophores lines the body margin from the hindgut to near the tail tip. Posterior to this ventral body pigment is a small unpigmented area. Posterior to the ventral unpigmented area (arrow in Figure 1) is the fleshy caudal extension characteristic of the species. Pigment on this extension is distinct from that on the rest of the body. It is scattered rather evenly dorsally and ventrally on the body and out on to the finfolds. The lateral midline of this area remains unpigmented.

Identification of the larvae was possible because of the link to the adults provided by the 114-mm SL transforming specimen captured in the same area. The 114-mm specimen has meristics (Table 2), hooked dorsal spines, and a fleshy protrusion of the lower jaw characteristic of adult *P. goodei* and pigmentation similar to the larvae described above. The fleshy caudal extension is more distinct than in the larvae. Gut length (28% SL) is proportionately shorter and snout length (26% HL) proportionately longer. Additional pigment occurs on the dorsal surface of the head posterior to the eye, on the snout, and in a line along the margin of the preopercle extending posteriorly from the angle of the lower jaw. The ventral gut melanophores are in a single row along the entire gut length. Body pigmentation is less pronounced than in the larvae but still distinct.

Adults of *P. goodei* are characterized by their extremely elongate body, the absence of a distinct caudal fin, and the presence of a fleshy protrusion at the tip of the lower jaw. When alive, the two Oregon specimens were brightly colored. The body was light green dorsally shading to yellow ventrally and orange on the throat. Two dark maroon, horizontal stripes were present laterally with maroon spots scattered over the entire dorsal surface. Several dashed maroon lines radiated posteriorly from the snout. A distinct maroon-colored, horizontal bar extended anteriorly from the margin of each eye half the distance to the snout tip. Morphometrics and meristics appear in Table 1. Gut length (29% SL) is similar to that for the transforming specimen, but the snout length (31-33% HL) is greater. Both specimens exhibited a vertebral anomaly in which the centra of two adjacent vertebrae were fused to form a single element with two neural and two hemal spines. In the 309-mm SL specimen the 160th vertebra was fused and in the 272-mm SL specimen it was the 169th element.

Occurrence

Collection data for *P. goodei* from Oregon waters is presented in Table 2. All specimens came from waters off the central coast of Oregon between March and August. All but one was captured during daylight. All but one was taken in water greater than 120 m deep on the continental shelf 18 km or closer to shore where the bottom was primarily gray sand.

TABLE 2.–Collection data for *Ptilichthys goodei* from Oregon waters.

SL (mm)	Date	Location		Km from coast	Coastal reference	Time	Bottom depth (m)	Tow depth (m)	Gear	Bottom type[1]	Surface temp. (°C)
		Lat. N	Long. W								
Larvae:											
20.3	25 Mar. 1973	44°00′	124°22.1′	18	Siuslaw River	1526-1542	117	100-0	Bongos	Gray sand-green mud	11.0
24.7	20 Apr. 1973	44°00′	124°22.1′	18	Siuslaw River	0235-0300	109	75-0	Bongos	Gray sand-green mud	10.4
36.0	14 May 1971	44°39.1′	124°17.7′	18	Newport	1621-1641	80	75-0	Bongos	Gray sand	11.2
Transforming:											
114	29 June 1971	44°39.1′	124°52.7′	65	Newport	1128-1153	340	150-0	Bongos	(Slope)	14.5
Adults:											
272	7 Aug. 1973	44°42′	124°7′	5	Moolach Beach	0945-1007	52	52	Otter trawl	Gray sand	9
309	3 July 1373	44°45′	124°14′	13	Cape Foulweather	1010-1028	80	80	Otter trawl	Gray sand	10

[1]From USC&GS Charts No. 5702 and No. 5802.

The larval and transforming specimens reported here are the only representatives of *P. goodei* found in 847 small-mouth (0.2 m) bongo and 413 large-mouth (0.7 m) bongo samples analyzed to date from waters off Oregon. The samples are part of an ongoing project to study seasonal and annual variations in distribution and abundance of larval fishes. Other studies of larval fishes off Oregon (Richardson 1973; Pearcy and Myers 1974) yielded no *P. goodei*.

The two adult specimens are the only ones recovered from 23 trawl samples taken during the summer of 1973 in conjunction with an ecological baseline study of the nearshore region of the mid-Oregon coast in the vicinity of Yaquina Head. Although they were taken with a bottom trawl, it is possible that the specimens entered the net shortly before it was brought on board. Thus, they may have been in near surface water rather than on the bottom as their presence in trawl samples would suggest.

Discussion

Vertebral counts, (53 to 55) + (172 to 174) = 227, of the transforming and adult Oregon specimens are lower than those, (58 to 59) + (179 to 182) = 238 to 240, reported by Makushok (1958), presumably for Bering Sea specimens. The counts are also lower than those, 236 to 240, given by Hart (1973), presumably for British Columbia specimens. This could indicate clinal variation with the southern specimens having fewer vertebrae. On the other hand, the lower number of both abdominal and caudal vertebrae of the Oregon specimens could indicate the presence of an undescribed species. Additional Oregon specimens are needed to determine the range of variation in vertebral number and to compare with northern specimens to see if they are actually the same species.

Reasons why quillfish have not previously been reported from Oregon waters are speculative. A partial explanation may be the lack of major sampling efforts in Oregon's coastal zone until recent years. Rarity (Makushok 1958; Hart 1973), inaccessibility, avoidance, and escapement also offer explanations. It is possible the adults bury themselves in the bottom (Makushok 1958) and are thus inaccessible to conventional types of gear. Behavior exhibited by one of the adults taken off Oregon suggests the quillfish may readily avoid and/or escape from trawl gear. Immediately after the trawl was brought aboard, the slender fish wriggled through the meshes of the net onto the deck of the vessel. It demonstrated great agility with snakelike undulations. The larvae may remain on or near the bottom, or they may spend all or part of the time in the neuston. Either situation would make them inaccessible to most plankton gear. The large size of the larvae indicates good avoidance capabilities.

Acknowledgments

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Literatured Cited

DeLacy, A. C., B. S. Miller, and S. F. Borton.
1972. Checklist of Puget Sound fishes. Univ. Wash. Sea Grant Publ. 72-3, 43 p.

Grinols, R. B.
1965. Check-list of the offshore marine fishes occurring in the northeastern Pacific Ocean, principally off the coasts of British Columbia, Washington, and Oregon. M.S. Thesis, Univ. Washington, Seattle, 217 p.

Hart, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can., Bull. 180, 740 p.

Hubbs, C. L., and K. F. Lagler.
1958. Fishes of the Great Lakes region. Revised ed. Cranbrook Inst. Sci., Bull. 26, 213 p.

Makushok, V. M.
1958. The morphology and classification of the northern blennioid fishes (Stichaeoidae, Blennioidei, Pisces). Proc. Zool. Inst., Akad. Nauk SSSR Tr. Zool. Inst. 25:3-129. (Translated by A. R. Gosline, Ichthyol. Lab., U.S. Fish Wildl. Serv., 1959, 59 p.; U.S. Natl. Mus., Wash., D.C.)

Pearcy, W. G., and S. S. Myers.
1974. Larval fishes of Yaquina Bay, Oregon: A nursery ground for marine fishes? Fish Bull., U.S. 72:201-213.

Quast, J. C., and E. L. Hall.
1972. List of fishes of Alaska and adjacent waters with a guide to some of their literature. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-658, 47 p.

Richardson, S. L.
1973. Abundance and distribution of larval fishes in waters off Oregon, May-October 1969, with special emphasis on the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 71:697-711.

Walker, E. T.
1953. Records of uncommon fishes from Puget Sound. Copeia 1953:239.

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EFFECT OF CROWDING ON STOCK AND CATCH IN *TILAPIA MOSSAMBICA*

In a previous report (Silliman 1972) I described the effect of crowding on the relation between exploitation and yield in *Tilapia macrocephala*. Subsequently I performed a similar experiment with *T. mossambica*. Since the results were somewhat different for the latter species and because of its wide use in pond culture, a brief report of the second experiment seems justifiable.

Apparatus and Procedures

Most of the procedures and apparatus were identical with those reported by Silliman (1972). Essentially the approach was to raise the populations in two conventional aquariums, one (L) with a volume of 155.2 liters and the other (S) with 77.6 liters so that S had exactly one-half the capacity of L. Aeration was by airstones and illumination by overhead fluorescent lamps. Rectangular spaces at the ends of the aquariums were fenced off with rods placed 3 mm apart, providing refuges for the young. Further shelter was provided by floats with suspended cords and by fiber brush shelters. Covering part of the aquarium walls with black plastic furnished shaded areas for spawning. Water condition was maintained by filtration and weekly partial water changes. Water temperature was 24° ± 2°C to month 5.7 and 30° ± 2°C thereafter. Feeding details are given in Table 1.

Populations were counted and weighed at approximately 2-mo intervals. Since *T. mossambica* is a mouthbreeder, it was desirable not to handle the fish more often than this. The 2-mo period includes 1.0 to 2.6 of the brood intervals reported by various authors (Kelly 1957, 30-40 days; Swingle 1960, 30-40 days; Uchida and King 1962, 23-61 days). Exploitation consisted of removing each 10th fish. In weighing, fish were drained in a net and placed in a previously weighed container of water; fish weight was total weight less the tare.

Table 1.–Food (in g) placed in tanks.

Day of week	Trout pellets		Tropical fish food		Total
	Moist	Dry	A[1]	B[1]	
Sun.	4.0	1.5	0.5	1.0	7.0
Mon.	5.5	1.5	0.5	1.5	9.0
Tues.	5.5	1.5	0.5	1.5	9.0
Wed.	5.5	1.5	0.5	1.5	9.0
Thurs.	5.5	1.5	0.5	1.5	9.0
Fri. A.M.	5.5	1.5	0.5	1.5	9.0
Fri. P.M.[2]	5.5	1.5	0.5	1.5	9.0
Total	37.0	10.5	3.5	10.0	61.0

[1]Commercial makes of dry food.
[2]This was combined with the Friday A.M. feeding in 35 out of 131 wk and with the Sunday feeding once.

Results and Conclusions

The two populations were started 10 July 1970 (Table 2, Figure 1). Recruitment (estimated from counts as in Silliman 1972) occurred after the temperature increase at month 5.7 and readjustment of the sex ratios at month 6.9 (Table 2). As was true for *T. macrocephala*, recruitment was greater in tank L (62) than in tank S (20). Some

TABLE 2.—Population and catch, *Tilapia mossambica*, in two sizes of tanks. Target exploitation rate was 10% per 2 mo.

	S—77.6-liter tank				L—155.2-liter tank			
	Number		Weight (g)		Number		Weight (g)	
Month[1]	Stock	Catch	Stock	Catch	Stock	Catch	Stock	Catch
0.3	[2]11	—	—	—	[2]11	—	—	—
0.5	[3]16	—	—	—	[3]16	—	—	—
4.1	[4]9	—	650	—	[4]9	—	593	—
6.9	[5]4	—	282	—	[5]4	—	303	—
9.2	20	—	372	—	50	—	529	—
11.1	20	—	641	—	49	—	571	—
13.1	20	—	831	—	46	—	754	—
15.2	20	—	983	—	44	—	900	—
17.0	20	—	1,088	—	46	—	1,006	—
19.1	20	2	1,154	119	46	5	1,081	115
21.2	18	2	1,121	108	41	4	1,047	113
23.0	16	1	1,120	146	36	4	1,071	100
25.1	14	1	987	89	34	3	1,070	100
27.1	12	1	912	90	31	3	1,083	198
29.2	10	1	861	114	29	3	1,043	119

[1]0 = 1 July 1970.
[2]Initial stocks were: S-6 immatures, 2 males, 3 females; L-4 immatures, 4 males, 3 females.
[3]To each stock, 5 immatures were added.
[4]Stocks were adjusted to 3 immatures, 2 males, and 4 females each.
[5]Stocks readjusted to 1 male and 3 females each. Temperature was increased from 24° to 30°C at month 5.7.

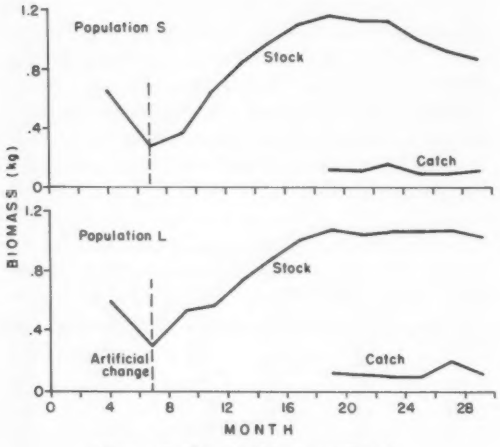

FIGURE 1.—Course of biomass and catch.

recruitment occurred throughout the experiment after month 6.9 in L but was limited to 2-mo period 6.9-9.2 in S.

Exploitation began at month 19.1 for both populations, at a target rate of 10% per 2 mo. Because of the small numbers of fish in the populations, actual percentages removed (Table 2) varied considerably from 10%. Populations differed in their response, S declining while L remained almost constant (Figure 1). Mean values of catch were S, 111 g; L, 124 g. Although the exploitation data were too few for firm conclusions, they suggest a greater yield from the larger tank, under the same catch rate and food amount. Here the response for *T. mossambica* was reversed from that found by Silliman (1972) for *T. macrocephala*. If significant, this difference may be due to the fact that *T. mossanbica* reaches larger ultimate size than *T. macrocephala*. The presence of a few large individuals in a population of small numbers (Table 2) could lead to a different response of the population to space available.

Literature Cited

KELLY, H. D.
1957. Preliminary studies on Tilapia mossambica Peters relative to experimental pond culture. Proc. 10th Annu. Conf. Southeast Assoc. Game Fish Comm., p. 139-149.

SILLIMAN, R. P.
1972. Effect of crowding on relation between exploitation and yield in *Tilapia macrocephala*. Fish. Bull., U.S. 70:693-698.

SWINGLE, H. S.
1960. Comparative evaluation of two tilapias as pondfishes in Alabama. Trans. Am. Fish. Soc. 89:142-148.

UCHIDA, R. N., AND J. E. KING.
1962. Tank culture of Tilapia. U.S. Fish Wildl. Serv., Fish. Bull. 62:21-52.

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THE OCCURRENCE OF ELVERS OF *SYNAPHOBRANCHUS AFFINIS* ON THE CONTINENTAL SLOPE OFF NORTH CAROLINA[1]

Members of the family Synaphobranchidae are demersal eels which are widely distributed in the Atlantic and Indo-Pacific oceans (Castle 1964). Data from a June 1973 cruise in the Norfolk Canyon area indicate that they are an important part of the fish community in both numbers and biomass in depths around 1,000 m (Virginia Institute of Marine Science unpubl. data). Bruun (1937) reported on the life histories and larval development of several synaphobranchids, and Castle (1964) listed synonomies in addition to keys to genera and species. Robins (1971) gave osteological, meristic, and morphometric data and also discussed the life history and ecology (Robins 1968).

Although Robins (1971) intensively examined 46 *Synaphobranchus affinis* Günter 1877 greater than 193 mm in total length, the occurrence of elvers or unpigmented juveniles of this species is unreported. The purpose of this report is to provide a record of capture, meristic and morphometric data, and some observations in food habits of *S. affinis* elvers.

Materials and Methods

A total of 89 elvers of *S. affinis* (Figure 1) were collected during a ½-h otter trawl haul from 1745 to 1815 h EST aboard the RV *Eastward* on 29 April 1973 at Eastward station 22039, lat. 34°03.2'N, long. 75°52.0'W at depths from 550 to 600 m. The gear used was a 30-foot shrimp trawl with a ¼-inch stretch-mesh cod end liner.

Total length of all specimens was measured to the nearest millimeter. A subsample of 40 elvers was taken for meristic analysis using a table of random numbers (Rohlf and Sokal 1969). Elvers were cleared in 2% potassium hydroxide, stained with alizarin red-S in 2% KOH, passed through a graded series of glycerine, and stored in 100% glycerine to which thymol was added. Three replicate counts were made of the following meristic characters: total vertebrae; dorsal, anal, caudal, and left and right pectoral fin rays; left and right branchiostegals. The presence and position of vertebral deformities (fused or partially fused vertebral centra; extra, fused, or distorted neural or hemal spines) were noted and representative types were drawn with the aid of a camera lucida.

To determine if osteological deformities might result in differential mortality of *S. affinis* during later life, 40 additional specimens ($\bar{x}$ total length = 220 mm, extremes 173-305 mm) collected on 13 June 1973 aboard the RV *Columbus Iselin* in 630 m of water with a 45-foot otter trawl at lat. 37°03.2'N, long. 74°34.1'W were examined. These fishes were X-rayed, vertebrae counted, and the presence or absence of deformities noted. Frequency of occurrence of deformities in elvers and larger fish were compared by X^2 analysis (Sokal and Rohlf 1969).

Morphometric measurements were taken following the method of Robins (1971) with either dividers and dial calipers or a binocular microscope fitted with a calibrated ocular micrometer.

Results and Discussion

Eels of the genus *Synaphobranchus* are characterized by confluent branchial apertures with a slitlike opening on the midline of the throat (Robins 1971). Synaphobranchid eels commonly encountered in trawls on the continental slope near Cape Hatteras, N.C. are *Synaphobranchus kaupi*, *S. affinis*, and *Ilyophis brunneus* (Markle 1972; Virginia Institute of Marine Science unpubl. trawl records). Members of this group show varying degrees of plasticity and overlap in morphometric characters but also show mean differences (Robins 1971). The specific identification of these elvers as *S. affinis*, therefore, was based on vertebral counts.

Mean, 95% confidence interval, and the frequency distribution of vertebral counts are shown in Figure 2. Vertebral counts of the 40 specimens had extremes of 130 and 136 with a mode of 134. This is within the range of values for 44 *S. affinis* given by Robins (1971) ($\bar{x}$ = 133.1, extremes 128-139) and outside the range of the other species of synaphobranchids common to this region (*S. kaupi*: $\bar{x}$ = 148.0, extremes 146-150; *Ilyophis brunneus*: $\bar{x}$ = 147.5, extremes 144-151). Means, 95% confidence intervals, and frequency distributions of other meristic characters are found in Figure 2. Paired t tests (Sokal and Rohlf 1969) showed no significant differences between the number of left and right pectoral fin rays (t = 1.00, df = 39) or the number of left and right branchiostegals (t = 0.42, df = 39). Dorsal and

[1]Virginia Institute of Marine Science contribution no. 652.

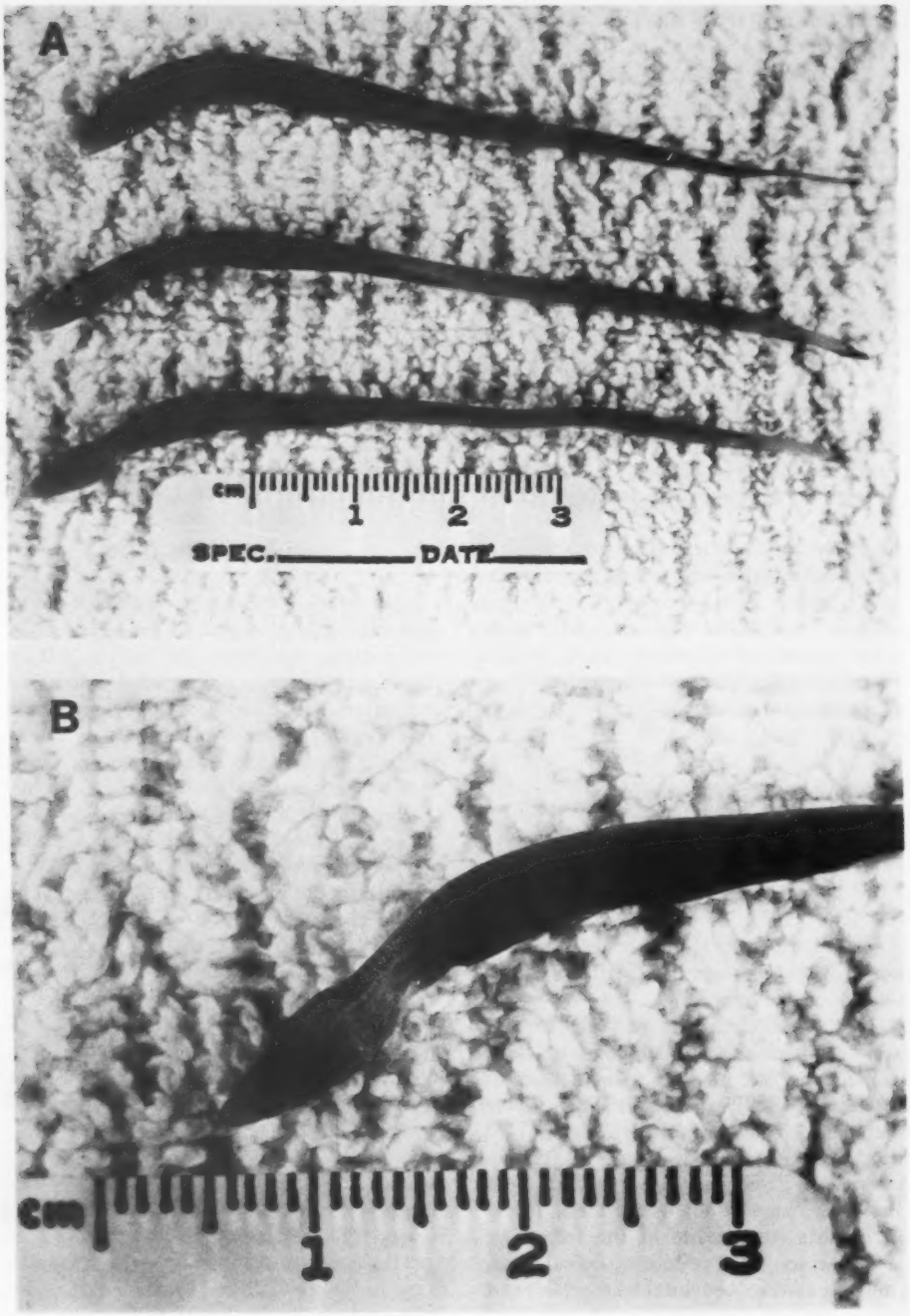

FIGURE 1.–(A) Photograph of a series of *Synaphobranchus affinis* elvers. (B) close-up view of anterior region of one elver of *S. affinis* showing dark, bluish-black peritoneum and slight pigmentation above lateral line.

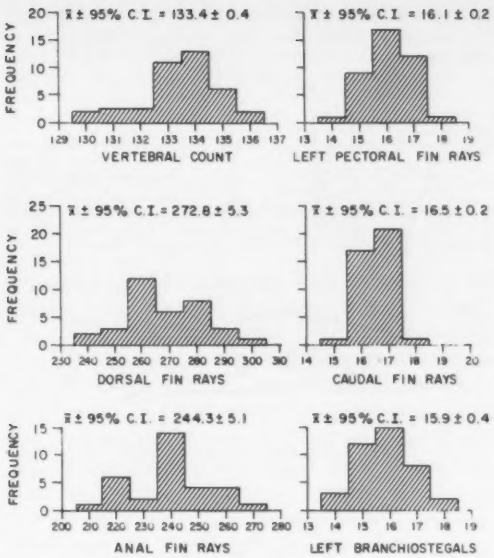
FREQUENCY
X̄ ± 95% C.I. = 133.4 ± 0.4
VERTEBRAL COUNT
X̄ ± 95% C.I. = 16.1 ± 0.2
LEFT PECTORAL FIN RAYS
X̄ ± 95% C.I. = 272.8 ± 5.3
DORSAL FIN RAYS
X̄ ± 95% C.I. = 16.5 ± 0.2
CAUDAL FIN RAYS
X̄ ± 95% C.I. = 244.3 ± 5.1
ANAL FIN RAYS
X̄ ± 95% C.I. = 15.9 ± 0.4
LEFT BRANCHIOSTEGALS

FIGURE 2.–Means, 95% confidence intervals (C.I.), and frequency distributions of various meristic characters of *Synaphobranchus affinis* elvers.

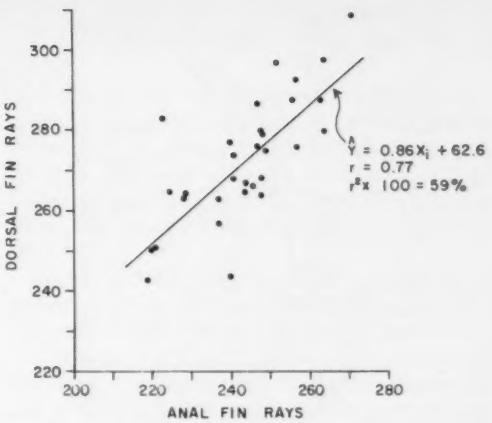

FIGURE 3.–Regression relationship between dorsal and anal fin rays of *Synaphobranchus affinis* elvers, where y = dorsal fin rays, x = anal fin rays, r = correlation coefficient, and $r^2 \times 100\%$ = coefficient of determination.

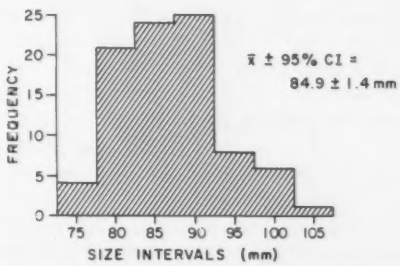

FIGURE 4.–Frequency distribution, mean, and 95% confidence interval (C.I.) of total length of *Synaphobranchus affinis* elvers.

anal fin rays showed a great degree of variability which is also characteristic of the American eel, *Anguilla rostrata* (Wenner 1972), and the snake eel, *Pisodonophis cruentifer* (Wenner unpubl. observations). Dorsal fin rays had extremes of 243 and 309 whereas anal fin rays had extremes of 219 and 271. Plots of dorsal against anal fin rays suggested a correlation and therefore the linear regression equation, correlation coefficient, and coefficient of determination were calculated (Figure 3). Fifty-nine percent of the variation in the number of dorsal fin rays was associated with the number of anal fin rays.

Mean length of the *S. affinis* elvers was 89 mm with extremes of 72 and 105 mm. Length-frequency distribution is found in Figure 4. Means, 95% confidence intervals, and extremes for morphometrical measurements are given in Table 1. All values fell within the ranges of those of *S. affinis* presented by Robins (1971).

Osteological deformities associated with the vertebral column were found in 72.5% of the 40 elvers and in 60% of the larger *S. affinis* examined. In both instances, most deformities were in the caudal part of the vertebral column, generally in the last 30 vertebrae. Illustrations of some representative deformities are shown in Figure 5 and a summary of the major types is in Table 2. X^2 analysis showed that there was no significant difference between elvers and larger immature fish (X^2 = 1.72, df = 39), suggesting that these deformities do not result in differential mortality in fishes possessing them.

It is conjectural whether these specimens

TABLE 1.–Summary of morphometric characters of elvers of *Synaphobranchus affinis*. C. I. refers to confidence interval.

Morphometric character	Mean ± 95% C.I.	Extremes	*n*
% total length			
Preanal length	27.7 ± 0.5	25.6-32.0	39
Predorsal length	30.0 ± 0.7	25.6-34.7	39
Head length	13.0 ± 0.2	11.3-14.2	40
% head length			
Gape length	66.9 ± 1.1	58.3-74.5	40
Horizontal eye diameter	16.8 ± 0.4	14.8-21.0	40

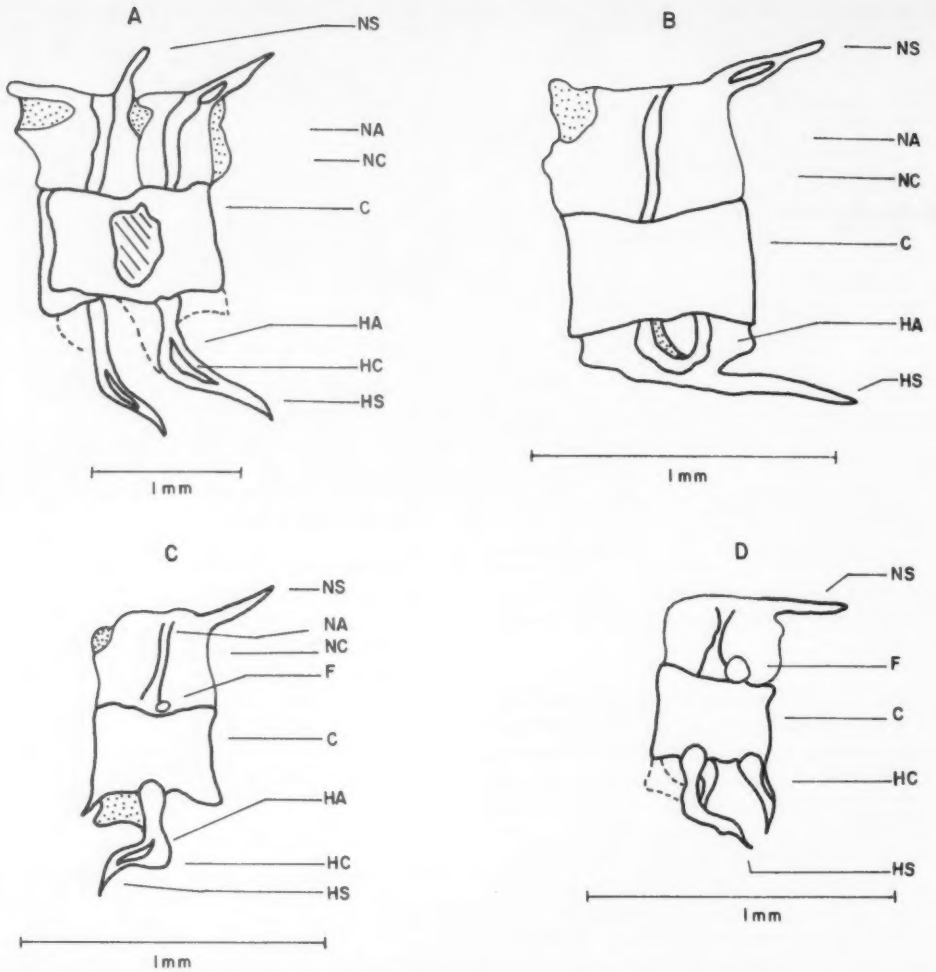

FIGURE 5.—Lateral views of various osteological deformities associated with the caudal vertebrae of *Synaphobranchus affinis*. Dashed lines in figures represent areas of incomplete ossification. NS = neural spine; NA = neural arch; NC = neural canal; C = centrum; F = foramen; HA = hemal arch; HC = hemal canal; HS = hemal spine; TL = total length in millimeters. (A) Fused centra with a bony knob projecting laterally; TL = 92. (B) Two sets of hemal spines which are fused together forming an arch; TL = 102. (C) Hemal spines projecting anteriorad rather than posteriorad; TL = 91. (D) Extra unfused set of hemal spines with one set projecting anteriorad and one set posteriorad; TL = 79.

represent the size at which the elvers descend to the bottom from the pelagic realm, where they pass their larval existence, because closing and mid-water nets were not used.

Of the 40 cleared and stained specimens, 12 had material in the gut cavity. Three contained crustacean appendages whereas nine had discernable fish remains such as disarticulated vertebrae. One elver contained an intact gonostomatid which had been swallowed head first. Gonostomatids are mesopelagic but the elver could have ingested it while in the trawl.

Acknowledgments

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TABLE 2.–Summary of the types of vertebral anomalies in *Synaphobranchus affinis* elvers expressed as percent of specimens with anomalies. The sum of the percentages is greater than 100% because some individuals had more than one type.

Item	Elvers	Larger immature fish
Sample size	29	24
Abnormal hemal spines	81.6	83.3
Abnormal neural spines	3.4	0.0
Fused or partially fused vertebrae	13.6	16.7
Multiple anomalies	57.8	16.7

I thank J. A. Musick of the Virginia Institute of Marine Science and D. M. Cohen of the Systematics Laboratory, National Marine Fisheries Service (NMFS), NOAA, National Museum of Natural History, Wash., D.C. for critical evaluation of the manuscript. B. B. Collette of the Systematics Laboratory, NMFS, NOAA, kindly provided X-ray facilities. R. Bradley illustrated the text and Ken Thornberry photographed the specimens. Thanks are also in order to my fellow students, Labbish Chao and D. Markle, for encouraging me to complete this project.

Literature Cited

BRUUN, A. F.
1937. Contributions to the life histories of the deep sea eels: *Synaphobranchidae*. Dana-Rep., Carlsberg Found. 2(9):1-31.

CASTLE, P. H. J.
1964. Deep-sea eels: Family Synaphobranchidae. Galathea Rep. 7:29-42.

MARKLE, D. F.
1972. Benthic fish associations on the Continental Slope of the Mid-Atlantic Bight. M. A. Thesis, Coll. William Mary, Williamsburg, Va., 68 p.

ROBINS, C. H.
1968. The comparative osteology and ecology of the synaphobranchid eels of the Straits of Florida. Ph.D. Thesis, Univ. Miami, Coral Gables, Fla., 149 p.
1971. The comparative morphology of the Synaphobranchid eels of the Straits of Florida. Proc. Acad. Nat. Sci. Phila. 123:153-204.

ROHLF, F. J., AND R. R. SOKAL.
1969. Statistical tables. W. H. Freeman and Company, San Franc., 253 p.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry. The principles and practice of statistics in biological research. W. H. Freeman and Company, San Franc., 776 p.

WENNER, C. A.
1972. Aspects of the biology and systematics of the American eel, *Anguilla rostrata* (Lesueur). M. A. Thesis, Coll. William Mary, Williamsburg, Va., 109 p.

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CATCHES OF ALBACORE AT DIFFERENT TIMES OF THE DAY

The purpose of this study is to examine the hypothesis that diel variations occur in the catches of albacore by boats trolling surface jigs off Oregon. Although albacore fishermen talk of "morning bites" and "evening bites," no published data exist, to our knowledge, confirming these trends.

Studies on the feeding habits of tunas, however, provide evidence for intense feeding activity during certain periods of the day. Based on the quantity of food in stomachs, Iverson (1962) concluded that major feeding periods of albacore occurred in early morning and late afternoon-evening. Similarly, Nakamura (1965) and Dragovich (1970) found evidence for morning and late afternoon peaks in the stomach fullness of skipjack and yellowfin tunas. Food consumption of captive skipjack was greatest between 0630 and 0830 h, and skipjack tuna in only one of three tanks fed intensively in late afternoon (Magnuson 1969). This was in agreement with Uda (1940) who reported that catches of skipjack tuna with pole and live bait peaked in early morning hours and were usually followed by successively lower peaks later in the day.

Fishermen were solicited to record data on 1969 and 1970 albacore catches in special logbooks. Several entries per day were requested. The records of five boats fishing off Oregon during July, August, and September 1969 were used for this study. These five skippers kept detailed records averaging eight entries per day. In 1970 the records of 12 boats were used that recorded catches at least every 4 h during the fishing day for 20 July-2 August 1970. All boats were 45-60 feet in length.

Average catches per boat were calculated for each hour fished, usually 0500-2200 h or 2300 PDT, for 3 mo in 1969 and 2 wk in 1970. When the interval between logged catches was greater than 1 h, the catch for the interval was divided by the number of hours fished, and this average number was distributed uniformly within the interval. Because the selected boats did not necessarily fish in the same locality or during the same days of the months, the data provide only an estimate of the general trends in hourly catches of albacore off Oregon.

The catches of albacore versus hours of the day are shown in Figure 1. Chi-square tests of the

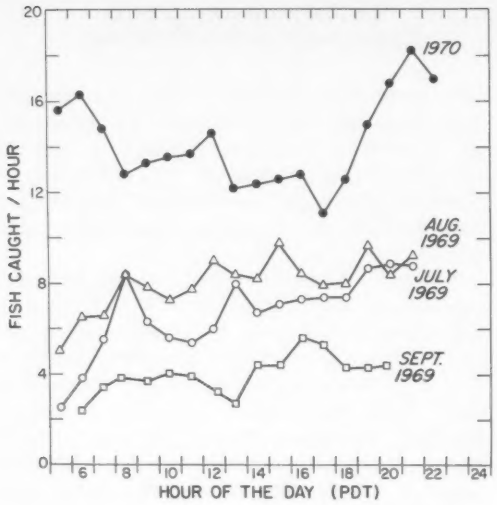

FIGURE 1.—Average catch of albacore per boat for each hour of the day from 0500 to 2200 for 3 mo in 1969 and for 20 July-2 August 1970. The numbers for hours of the day refer to the time at the beginning of the interval.

heterogeneity of catches for all four of the data sets are significant ($P<0.05$), indicating that catch rates were not constant with time but varied throughout the day. Consistent trends for diel periodicity in catches, however, are not apparent.

Only during 1970 was there an obvious trend for peak catch rates to occur early in the morning and in the evening. These peaks coincided with the local mean times of sunrise and sunset (about 0600 and 2100 PDT).

The separate months of 1969 show a variable pattern with peaks occurring at different times during different months. There is no evidence for a pronounced early morning "bite," except perhaps 0800-0900 in July. Catch rates generally increased with time during the day. Most 1969 afternoon catch rates were above the median for each of the 3 mo, but they were not markedly higher in the evening as was found for 1970.

The catches during 1970 were exceptionally high. Even the lowest 1970 catch rate was higher than any of the peak 1969 catches (Figure 1). The 1970 jig-boat season for albacore off Oregon was unusually short (most fish were caught between 22 and 29 July) and the fleet was localized in a small area (Pearcy 1973; Keene 1974). For those reasons, the spatiotemporal variability for the 1970 data is probably much less than for the separate months of 1969.

From our limited data we conclude that albacore feed throughout the day. Catch rates averaged over several weeks do not always indicate morning and evening periods of intense feeding. Obviously this does not preclude the occurrence of morning and/or evening bites in some areas on some days.

Although stomach fullness and catch rates are both related to feeding behavior, they may provide different results on feeding periodicity because of the influence of such factors as changes in depth distributions, vulnerability to fishing methods, and the times required for accumulation and digestion of food in the fish's stomach. For example, the especially high rates of capture of albacore on surface jigs during sunrise-sunset periods of 1970 may be related to the vertical migration of Pacific saury, *Cololabis saira*, their major prey during this time (Pearcy 1973). Saury migrate to surface waters at sunset and descend into deeper waters at sunrise (Hotta and Odate 1956; Hughes and Gill 1970). Relatively low catch rates during the day may therefore be the result of either albacore pursuing saury into deeper water where albacore are less vulnerable to surface lures or to reduced feeding activity.

Acknowledgments

We thank the albacore fishermen who made this study possible. This research was part of the Oregon State University Sea Grant Program, supported by NOAA Office of Sea Grant, Department of Commerce under Grant No. 04-5-158-2.

Literature Cited

DRAGOVICH, A.
1970. The food of skipjack and yellowfin tunas in the Atlantic Ocean. Fish. Bull., U.S. 68:445-460.

HOTTA, H., AND K. ODATE.
1956. The food and feeding habits of the saury, *Cololabis saira*. [In Jap., Engl. abstr.] Bull. Tohoku Reg. Fish. Res. Lab. 7:60-69.

HUGHES, S. E., AND C. D. GILL.
1970. Saury is promising 'new' fish on west coast. Natl. Fisherman 50(12):12C-14C.

IVERSON, R. T. B.
1962. Food of albacore tuna, *Thunnus germo* (Lacépède), in the central and northeastern Pacific. U.S. Fish Wildl. Serv., Fish. Bull. 62:459-481.

KEENE, D.
1974. Tactics of Pacific northwest albacore fishermen-1968, 1969, 1970. Ph.D. Thesis, Oregon State Univ., Corvallis, 93 p.

MAGNUSON, J. J.
1969. Digestion and food consumption by skipjack tuna (*Katsuwonus pelamis*). Trans. Am. Fish. Soc. 98:379-392.

NAKAMURA, E. L.
1965. Food and feeding habits of skipjack tuna (*Katsuwonus pelamis*) from the Marquesas and Tuamotu Islands. Trans. Am. Fish. Soc. 94:236-242.
PEARCY, W. G.
1973. Albacore oceanography off Oregon – 1970. Fish. Bull., U.S. 71:489-504.
UDA, M.
1940. The time and duration of angling and the catch of "Katsuo", *Euthynnus vagans* (Lesson). Bull. Jap. Soc. Sci. Fish. 9(3):103-106. (Engl. transl. 1951, U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 51:12-17.)

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